

Towards Resolving the American and West African Strombidae (Mollusca: Gastropoda: Neostromboidae) Using Integrated Taxonomy

Stephen J. Maxwell,¹ Aart M. Dekkers,² Tasmin L. Rymer^{1,3} and Bradley C. Congdon^{1,3}

¹ College of Science and Engineering, James Cook University, Cairns Qld 4870

stephen.maxwell@my.jcu.edu.au

² Oasestraat 79, 1448 NR Purmerend, The Netherlands

aart.dekkers@wxs.nl

³ Centre for Tropical Environmental and Sustainability Sciences,
James Cook University, Cairns Qld 4870, Australia.

tasmin.rymer@jcu.edu.au

brad.congdon@jcu.edu.au

ABSTRACT The phylogeny of the American Strombidae the genus *Lobatus* is limited to the extant *Lobatus raninus* and several fossil precursors, the genera *Macrostrombus*, *Aliger* and *Titanostrombus* are re-installed as valid genera. The genus *Persististrombus* which was used as a sink for a plethora of species, is limited to the extant *Persististrombus granulatus*, fossil American species and a few Eocene to Miocene European species, which we enclose within *Persististrombini nov. tribus* along with *Thetystrombus*. Two new genera for the Miocene ancestral basal taxa of *Aligerini nov. tribus*, *Edpetuchistrombus nov. gen.* and *Antestrombus nov. gen.*, both of which represent basal reference points enabling greater clarity in the resolution of early West African and American Strombidae radiations are proposed. This revised phylogeny informed by total evidence and historical revisions will assist in providing an evolutionary-based nomenclature that offers a structural basis for further explanation of the radiation and diversification of taxa within the Strombidae.

KEY WORDS Crown clade, East Africa, Strombidae, *Edpetuchistrombus*, *Antestrombus*, taxonomy, Western Atlantic

INTRODUCTION

Higher taxonomic classifications provide a framework for the ordering of species, and with the introduction of the PhyloCode, a revolution in the way that the nomenclature is formed is coming. This paper deals with the three forms of naming that can be applied to higher taxonomic groups and applies Bryant's (1996) conventions for the defining of higher taxa. Bryant's guidelines are practically applied to the resolution of the taxonomy of West African and American Strombidae. We first examined the literature and determined relational clades for this group based on molecular and internal and external morphological relationships, and then

integrated these relationships in the standard type-based nomenclature. These relationships were contextualised with reference to ancestral relationships from the fossil record to formulate a theory of American Stromboid radiation. Associations between these clades were then defined using either stem or nodal definitions conforming to the principles of phylogenetic nomenclature. We also compared similarity-derived maximum-likelihood tree generated using combined histone 3 and cytochrome oxidase I data versus cytochrome oxidase I alone and found no difference in the level of taxonomic resolution achieved. We defined an anatomical character set which was much smaller through the removal of multiple

homeoplasies, this reduced character set had the same resolution as previous studies where those homeoplasies were included. Following construction of these trees, we mapped the published type-based taxonomy on the trees generated during the analyses to provide an insight into how alternative forms of evidence support current taxonomic understanding reflected in the nomenclature. All evidence from the relational clades and mapped taxa were considered, and a phylogeny explaining the internal relationships within the West African and American Strombidae was derived.

The West African and American Strombidae Rafinesque, 1815 have seen many taxa shuffled between genera as workers revise their understanding of morphological character relations. This rearranging of taxonomic relationships has led to cladistic instability and resulted in confusion in the nomenclature. This confusion is attributable to a major failing of modern taxonomic practice, in that it belies apomorphy-based definitions that define higher nomenclature, irrespective of the total evidence available (Latiolais *et al.* 2006; Dekkers 2008a, 2008b).

To resolve this issue and provide taxonomic clarity for the group, this review redefines the infra-familial relationships within the American and West African Strombidae Rafinesque, 1815, based on a new approach to higher taxonomic practice (Bryant 1996). In doing so, it provides a practical example of how clades are resolved and defined so as to provide a nomenclature that is stable. This stability comes with the grounding of the nomenclature in a well-resolved phylogeny and avoids the long-term problem of revisions generating paraphyletic higher taxa of older classifications (Abbott 1960, 1961; Latiolais *et al.* 2006).

We herein review the concept of clades and how they are formulated. We consider the rank of genus and subgenus as clades, as they form the first points where taxa are aggregated taxonomically. We argue that the currently accepted phylogeny of American and West African Strombidae is simplistic and is based on either a misunderstanding of the potential for reticulation among evolutionary units, or on the over-reach of generic inclusivity. These faults are grounded in a limited systematic approach that uses a purist biological concept of species but is morphologically defined in terms of criteria. This approach restricts the potential for a greater understanding in terms of a more taxonomically relevant nomenclature. We see no differentiation in the historical use of taxa at the levels of subgenera and genera for the purposes of clade recognition in this paper, as the names in use at these levels are often shuffled up and down cladistically. Therefore, we treat subgenera and genera as ranks, and application is governed by the zoological nomenclature codes on types and priority.

THE THEORY OF HIGHER CLASSIFICATION

Higher classification in biology has two fundamental roles: it provides a practical definition for the ordering of the reference list of species, and it provides a diagnosis that describes how that list can be derived (Benton 2000). Therefore, the role of higher classification is to elucidate the evolutionary relationships between organisms and serve to provide a tool for comparative evolutionary analyses (de Queiroz and Gauthier 1990; Benton 2000). Furthermore, the diagnosis is supplemented with a description that states the innate characteristics of the organisms that are to be included within a particular rank, enabling a high level of clarity on what is, or is not, to be

included within the erected clades (de Queiroz and Gauthier 1990).

Ranks have historically been based on a need to recognise the phenotypic variability of organisms that are included under each classification and have sought to encapsulate the innate breadth and uniqueness of the characters of the organisms included (Ereshefsky 2002). Furthermore, the problem with characters is that they create ambiguity, and this leads to problems of delineation in what is naturally a continuous process of evolutionary linkage within a phylogenetic system. Hennig (1965) argued for, but later abandoned, the idea that higher taxa need to be grounded by a taxon drawn from the particular time from which the lineage arose. Furthermore, the lack of explicit time grounding avoids arguments for the need to identify the monotypic origins of higher taxa and limits the subsequent inferred nature of nodal taxa to the organisms used in its definition (Platnick 1977). Cladistic analysis needs to find the point of equivalence at which there is maximum descriptive ability and maximum explanatory power, providing the optimal delineation of a taxon (Platnick 1986).

Rank hierarchy seeks to achieve a level of positioning of a taxon relative to another that allows the creation of a class of taxa that then forms the underlying argument for ranking and subsequent ordering of the natural system (Stevens 2002). Therefore, taxa and their ancestral relationships cannot be discerned from assigned higher Linnaean ranks, which are necessary under the restrictions of that system, as they are not grounded in the phylogeny of the organisms. Linnaean ranks serve no other purpose than to group 'like' organisms. The nineteenth century concepts of adaptation, in particular the ideas of Lamarck and Darwin, were yet to be formalised when Linné formulated the system of nomenclature. This

lack of theoretical importance given to the asymmetry of ranks under the Linnaean system of nomenclature has led to the lack of evolutionary justification in tree topology and nomenclature, resulting in the assignment of higher taxa within the nomenclature that provide no insights as to the evolution of the organisms that are being classified. Therefore, there is a need for a complete restructure of the higher nomenclature (de Queiroz and Gauthier 1990, 1992, 1994; de Queiroz 1996). That is, under the Linnaean system of nomenclature, when a genus is compared to other genera, there is an implicit equality in rank, which in terms of an evolutionary grounded phylogeny, may not actually be equal.

In contrast to Linnaean nomenclature, phylogenetic nomenclature is designed to show relationships based upon a historically or evolutionary generated phylogeny. This hierarchical approach to the ordering of nature creates taxon-bearing reference points that then form the basis for relative comparisons, without any implications for the existence of ranks (Stevens 2002). Brochu and Samrall (2001) emphasize the benefit of explicitness and that universal meaning needs an explicit taxon name definition. That is, under phylogenetic nomenclature, name-bearing reference-points are used in formal definitions that are restricted by a diagnosis, thus enabling stable internal tree reconstruction (Schander 1998). This is in contrast to Linnaean nomenclature, where the assignment of taxa is singularly explicit in all definitions lacking relational explanations, thus giving rise to inherent paraphyletic problems. In contrast, phylogenetic nomenclature is fundamentally implicit. Instability in definition as a result of implicit description where relationships are given priority is only found if the definition fails to fulfil all the requirements needed to satisfy that formal definition (Benton 2000).

The use of structured or formulaic styled definitions for cladistic relationships brings clarity to the relationship between name and taxon in taxonomic definitions (Benton 2000). Much of the opposition to the acceptance of phylogenetic nomenclature is related to the misconception that it causes a loss of taxonomic freedom to deviate taxa outside the definitional framework (Lidén and Oxelman 1996; Lidén *et al.* 1997; Bryant and Cantino 2002). The disruption to the use of the nomenclature in the real world that may occur with the adoption of a phylogenetic rank-free system and the subsequent changes in nomenclature that result from different approaches to the construction of phylogenies, can be minimized if the existing type-based taxa has priority in determining the named regions of inclusivity. The use of types can avoid such instability by providing stable markers for defining the limits of inclusivity (Blackwell 2002).

Recent works that apply phylogenetic nomenclature to biological revisions have demonstrated that streamlined transitions from traditional Linnaean nomenclature to relationship-based phylogenetic nomenclature can be achieved (Cantino *et al.* 1997; Pleijel 1999; Härlin and Härlin 2001). In order to avoid ambiguity in the definition of a clade there needs to be accuracy in the wording of the definition, avoidance of reference inspecificity, and provision of phylogenetic definitions of included taxa (Bryant 1996).

Practical Definitions in Higher Taxonomy

With the soon to be introduced PhyloCode set to revolutionize the way in which definitions are used in taxonomy, a review of the principles that govern the defining of clades needs to be explored. There are three ways a clade can be defined in higher taxa: first, node-based, where the most common ancestor of two terminals or

clades and all their descendants are included; second, stem-based, where all taxa more closely related to an organism than to another are included; and third, apomorphy-based, where all taxa that share particular unique characters are included (de Queiroz and Gauthier 1990, 1992, 1994; Bryant 1994; de Queiroz 1996; Sereno 1999; Benton 2000; Bryant and Cantino 2002).

The node-based structural definition is defined in terms of the point of delineation of two or more taxa from a common ancestor (de Queiroz and Gauthier, 1992; Sereno 1999). Any node-based definition must use taxa that are least inclusive and well nested within the clade to avoid relocation and internal inconsistency resulting in the creation of impossible clades (de Queiroz and Gauthier 1990; Schander and Thollesson 1995; Sereno 1999; Bryant and Cantino 2002). The use of names of multiple subordinate taxa in the node-based definition is only an issue in terms of stability if the taxa used in the definition are poorly supported (Sereno 1999; Bryant and Cantino 2002). All taxa that are basal need not be included. However, the definition needs to comprise enough basal taxa to avoid a more reduced inclusive clade than was originally intended. This use of designated phylogenetic context (Bryant and Cantino 2002), is a means of maximizing stability within a node-based definition. Cantino *et al.* (1997) outlined recommendations in the definition in order to maximize stability. First, there must be a level of 'substantial evidence'. Without this, there would be confusion through proliferation of phylogenetic synonyms. Second, a taxon whose membership is questionable should be avoided. Third, Sereno (1999) argued that the numbers of inclusive taxa used in the definition is dependent upon whether the clade content is well supported and nested. The use of well-supported and nested taxa will increase the

clade stability even as taxa are internally redistributed.

The stem-based structure for naming clades is based on the closer relationship between an ancestral taxon and its descendants than to more distant taxa (de Queiroz and Gauthier 1992; Sereno 1999). The stem-based definition in phylogenetic nomenclature is suited to revisions that have a lack of prior tree resolution (de Queiroz and Gauthier 1990; Sereno 1999; Bryant and Cantino 2002). The use of stem-based nomenclature also allows future division of all levels of taxa, and free movement within, or out of, a particular clade, which in turn eliminates the restrictions that the assignment of apomorphy and node-based definitions create. Dyke (2002) suggested that the movement of taxon would cause greater inclusion than the definition intended if the taxon that is used in the definition is involved in the movement. However, in his example of theropod dinosaurs, the principle concerns were of synonymic duplication as resolution increases. This is an issue for stem-based definitions only if 'proper' formulation of the principle definition from the start is lacking. Therefore, Dyke (2002) failed to recognise stability and unambiguous interpretation as having priority. It is only when priority is given to stability and clarity that the problem of proliferation of unnecessary definitions can be overcome, a concern of those who would oppose phylogenetic stem-based definitions (Dyke 2002). The stem-based definition grants higher significance to terminals, avoids ranking into unnecessary Linnaean categories, gives priority to clades, irrespective of characters and the need for inclusiveness, and is determined principally by historical phylogeny (Härlin 1999).

The apomorphy-based definition of a clade is based on the synapomorphy of the first ancestor in which it arose and includes all its descendants

(Sereno 1999; de Queiroz and Gauthier 1992). The use of apomorphy-based definitions in phylogenetic nomenclature is a major area of contention (Bryant 1994; Schander and Thollesson 1995; Pleijel 1999; Sereno 1999; Bryant and Cantino 2002). The apomorphy-based structure seeks to directly tie the actual empirical evidence to the recognition of taxa (Pleijel 1999). However, it is a fundamental concept to the study of taxonomic biology, with the focus on historicity rather than morphology that makes apomorphy-based definitions principally non-evolutionary (de Queiroz and Gauthier 1992). Bryant (1994) argued for the avoidance of apomorphy-based definitions. The restriction that this definition imposes upon the tree structure, and patterns that are absent in node and stem-based definitions, is the major fallibility in this descriptive approach. Apomorphy-based definitions are fundamentally flawed because they rely on homoplasy to allow cladistic discernment, with the actions of evolutionary processes that cause the loss of primary apomorphs, and levels of continued congruence with other apomorphs of near taxon. While Bryant and Cantino (2002) rightly point out that apomorphs do have a role in phylogenetic nomenclature, their use should be incorporated into either node or stem-based definitions as a means to give added stability.

BRYANT AND CROWN CLADE DEFINITIONS

A crown taxon differs from other taxa formulations by its definition being restricted to living taxa that have an immediate extinct outgroup (Sereno 1999). While it is possible to describe a crown taxon or clade with a stem-based definition, the inadvertent use of a node-based definition is the form most widely encountered within the nomenclature (de Queiroz and Gauthier 1992; Rowe and Gauthier 1992; Wyss and Meng 1996). The use of crown

clades is common in much of the taxonomy, but this does not necessarily improve taxonomic clarity or stability unless it is accompanied by a structured definition (Lee 1996). The aim must be for the taxonomist to obtain maximum stability, and the definition of a crown clade must be determined by the state of resolution of the basal dichotomy (Sereno 1999). The use of a crown clade as a mode of definition does not preclude the recognition of ancestral taxa within it, only that these taxa are not used in the formulation of the definition. Bryant (1996) argued for eight conventions that facilitate effective phylogenetic taxonomic definitions of clades:

1. *Phylogenetic definitions should name clades identified through phylogenetic analysis.*

There needs to be an explicit phylogenetic context and pattern to the naming of a clade (de Queiroz 1994). Clades need to have a basis in evolutionary fact that supports their erection. It is unnecessary to generate ranks within a hierarchy that are “space fillers” and do not contribute to the evolutionary contextualisation of the nomenclature.

2. *Phylogenetic definitions should have standardised formats.*

There needs to be a standardised format in the naming of taxa. The use of a stem or node-based definition is the individual concern for the taxonomist and is dependent on the level of resolution of the clade under consideration (Sereno 1999). A clade that has a high level of internal resolution is more suited to the node-based definition, and is independent of outgroup relations, compared to a clade that has a low level of internal resolution, which is more suited to a stem-based definition.

3. *Typification of taxa is an optional heuristic device for standardising hierarchical relationships among clades with particular taxon names.*

It is not necessary to include a terminal taxon in the definition at every level of the hierarchy, with higher order taxonomic ranks being sufficient if inclusivity is codified (Cantino *et al.* 1997). While the use of types is redundant in phylogenetic taxonomy, as the diagnosis fulfils the role of grounding the rank in the real world, types may assist with the standardising of hierarchical relationships and in defining the most inclusive taxa (de Queiroz and Gauthier 1992; Sundberg and Pleijel 1994; Bryant 1996). Bryant (1994) argued that, for a definition to achieve accuracy, there needs to be an explicit reference to a single common ancestor in the wording. Bryant (1994) also argued that providing an ancestral basis upon which a clade is grounded needs to be with the inclusion of “most recent”, which has significant implications for the clade structure that is chosen. A clade with a poorly resolved basal relationship is best defined by a stem-based definition because the reference upon which it is founded is based on outgroups, which by definition implicitly creates the ancient ancestor. Another ambiguity in wording is created when the definition of a crown clade is dependent on the current non-extinction of members, where future extinctions would change the clade definition (Lucas 1992). This problem can be avoided if the terms ‘extant’ and ‘living’ are not used in the definition (Bryant 1994, 1996). This allows evolution of the definition and retains stability in meaning while losing extant taxa to extinction. Tautology also causes a level of ambiguity in the wording of cladistic definitions (Bryant 1996).

4. *Emendation of phylogenetic definitions is necessary in particular instances but should preserve the association between taxon names and clades.*

The need for emendation of cladistic names is often required when there is confusion in the wording of the definition and where there is a lack of clarity in meaning, or appropriateness of the taxa that are included (Bryant 1996). This is particularly relevant as the suffixes used under the codes for nomenclature that are attached to a name may not truly reflect the organizational position when contextualized with evolutionary evidence. There are no ICZN rules governing the use of prefixes, but the inclusion of "Neo+type taxon" is advantageous to the recognition that a crown clade has been defined. This was the basis for the erection of Neostrombiodae: Prefix + type genus + suffix: Neo + Stromb + oidae for the epifamily rank.

5. *Crown clades should have "widely known taxon names".*

Where possible, existing taxonomic crown clade names should be retained in order to maintain stability. The current state of taxonomy often reflects the underlying phylogenetic understanding, albeit tied to ranks that obscure this. Therefore, a revision may involve a review and possible rejection of rules of priority in the ordering of ranks in nomenclature to save this taxonomy (Rowe 1998; de Queiroz and Gauthier 1992; Anderson 2002). This can be achieved if names are crown clades (Bryant 1996). The issue of implied ranking based on the Linnaean suffix means that the suffix should be amended to reflect the nature of the definition (convention 8 *vide infra*). Cantino *et al.* (1997) argued that current suffixes utilised by existing taxonomy could be maintained to avoid unnecessary changes and make the shift to a phylogenetic system more acceptable. In

addition, taxonomists familiar with a particular taxon would still be able to recognize the cladistic group that is implied, irrespective of the suffix.

6. *Given several "widely known taxon names" that could be used for a crown clade, the one at the lowest rank in the Linnean hierarchy should often be chosen.*

If more than one name is available within the Linnaean hierarchical system, then the lowest rank should be applied. This would leave the higher ranks available for use for more inclusive clades (Bryant 1996).

7. *Stem-based taxon names could be formed from the name of the appropriate less inclusive node-based taxon and an appropriate suffix.*

The use of a suffix should be used to indicate whether the definition is based on the node, apomorph, or stem structure. De Queiroz and Gauthier (1992) suggested *-gens* or *-genea*, and Bryant (1996) suggested *-morpha* or *-formia*. However, recent revisions make the use of these suffixes somewhat problematic due to an inconsistent application to one level of rank as internal clade structures change (Bryant 1996). Furthermore, the conflagration of stem and node names, with shifts in stem structure, may obscure the evolutionary meaning that each different approach to formulating a definition brings. In the present paper, stems are formulated in order of nomenclatural position under the ICZN (1999).

8. *Taxon names should have recommended usages.*

Bryant (1996) argues that there may be a limitation of the use of names to particular contexts, and this may reflect the level of

meaning intended at the time by the taxonomist formulating the definition. That is, there may be a need to restrict the inclusivity of a definition as the understanding of the phylogeny expands and more taxa are brought into a particular cladogram.

TARGET TAXA AND THEIR HISTORICAL GENERIC AFFILIATIONS

We examined the taxonomy attributed to extant Strombidae Rafinesque, 1815 on the West African coast and in the Americas, and explored how the nomenclature of the subfamilies, genera, subgenera of those taxa reflects and explains the current evolutionary understanding of the relationships between those taxa. We used fossil taxa to define basal clades and to provide markers for understanding Atlantic radiations.

A list of all extant American and West African Strombidae Rafinesque, 1815 currently in general use was formulated. Each taxon was revised in order of date of description using first principles. From this list of species, their current cladistic checklist of taxa and their cladistic position was confirmed by literature review to enable a basic framework upon which to commence the revision (Table 1). Where necessary the taxonomic list was updated as the revision and higher taxonomic relationships identified were resolved and defined. All amended taxonomic positions were applied retrospectively throughout. This enabled the discussions throughout to reflect the current taxonomy and to avoid nomenclatural confusion within the text, particularly with taxa that have been moved repeatedly between genera. The checklist, therefore, represents the currently accepted living species and their generic placement (Table 1). We focused on supra-specific ranks, hence forms and subspecies were omitted. An overview of the taxonomic ranks

from subfamily to genera is presented as the systematic part of this paper.

There is a significant level of taxonomic inflation in the supra-species nomenclature. In particular, this has involved the elevation of subgenera to genera, and the displacing of the unifying genus *Strombus* Linné, 1758. We do not deal with the arguments for or against the position of infra-subtribal ranks. Rather, we treated them all based on definitional form, and they were discussed and applied appropriately and equally without rank bias. The genus and subgenus are the basal ranks, defined as the first aggregative rank in systematics.

CURRENT TAXONOMIC RELATIONSHIPS

There have been four major systematic revisions on the nature of stromboids after Abbott (1960, 1961). Latiolais *et al.* (2006) based their work on a mix of morphology and genetics. However, the sample used was small and not representative of the diversity across the stromboid complex. Simone (2005) utilized anatomical information. However, only American and Caribbean taxa were studied. Bandel (2007) and Dekkers (2008a, 2008b) used morphology, fossil and geographical relationships, and Dekkers (2008a, 2008b) based much of his revision on the phylogeny generated by Latiolais *et al.* (2006). When these four approaches are compared, some well-defined clades are clear over all, which enable the contextualization of more focused monographs and papers within the broader clade structure (Figure 4). There have been a number of other smaller targeted monographs and papers that have contributed to understanding aspects of the cladistic relationships between West African and American taxa, and these fall into two groups: those grounded in a phenetic approach (Clench and Abbott 1941; Abbott

1960); and those that use morphology and some form of spatiotemporal evidence (Petuch 1994).

Latiolais *et al.* (2006) and Simone (2005) determined *Strombus* Linné, 1758 to contain *Strombus pugilis* Linné, 1758, *Strombus alatus* Gmelin, 1791 and *Strombus gracilior* Sowerby, 1825. Bandel (2007) combined *Strombus pugilis* Linné, 1758 with another species, *Macrostrombus costatus* (Gmelin, 1791) into the clade *Strombella* Schlüter, 1838. However, the inclusion of *Macrostrombus costatus* (Gmelin, 1791) within *Strombella* Schlüter, 1838 is problematic as it is contrary to the phylogenies presented by Simone (2005) or Latiolais *et al.* (2006) that hold for independent lineages. Clench and Abbott (1941) lumped all the Caribbean taxa within the clade *Strombus* Linné, 1758, a classification that fails to offer an explanatory reflection of the taxonomy in the nomenclature, which is a reflection on the taxonomic thinking of that time.

Latiolais *et al.* (2006) singled out *Strombus* (*s.l.*) *granulatus* (Swainson, 1822) and placed it in *Lentigo* Jousseaume, 1886. In contrast, Bandel (2007) and Dekkers (2008a) placed this taxon within *Persististrombus* Kronenberg and Lee, 2007. Similarly, *Thetystrombus latus* (Gmelin, 1791) has been shuffled with the family phylogeny during revisions, having been included in both *Lentigo* Jousseaume, 1886 (Abbott 1960) and *Persististrombus* Kronenberg and Lee, 2007 (Harzhauser and Kronenberg 2013). With the description of *Thetystrombus* Dekkers, 2008, the evolutionary understanding of the Strombidae Rafinesque, 1815 was enhanced through the provision of a West African focal point on which to base radiation theory.

The most contentious internal relationships are those within the clade identified as *Tricornis* Jousseaume, 1886 by Latiolais *et al.* (2006).

The use of this name is systematically problematic and reflects the broad lumping of species under the revisions of Abbott (1960). The genus *Tricornis* Jousseaume, 1886 (type – *Strombus tricornis* Lightfoot, 1786) currently contains two species (Bandel 2007; Dekkers 2008a), namely: *Tricornis tricornis* (Lightfoot, 1786) and *Tricornis oldi* (Emerson, 1965), considered restricted to the Indo-Pacific region (Bandel 2007).

Bandel (2007) was not so conservative in dividing up the West African-American complex, erecting three subgenera of *Strombus*: *Strombella* Schlüter, 1838 (type – *Strombus pugilis* Linné, 1758) *Mondactylus* Klein, 1753 (Type – *Strombus gallus* Linné, 1758) and *Eustrombus* Wenz, 1939 (sic = 1940) (Type – *Strombus gigas* Linné, 1758). The American stromboid taxonomy of Bandel (2007) is problematic because it does not reflect upon the cytochrome oxidase I (COI), or anatomically derived phylogenies (Latiolais *et al.* 2006; Simone 2005), which were already available, nor was it supported by Dekkers (2008a, 2008b). The use of *Aliger* Thiele, 1929 (Type – *Strombus gallus* Linné, 1758) over its junior synonym *Eustrombus* Wenz, 1940 (Type – *Strombus gigas* Linné, 1758) is correctly reflected in other revisions (Bandel 2007, Simone 2005). The use of *Lobatus* Iredale, 1921 for some members of the *Aliger* Thiele, 1929 shows a lack of understanding of the original definition of *Lobatus* Iredale, 1921 and its sister genera (Dekkers 2008b).

It is clear that the ongoing shifting of internal cladistic relationships in this complex is largely justified by the use of only a single form of evidence. The names that are applied to these clades vary, and this reflects the opinion of each taxonomist, and their understanding of what is the internal relationship, which can compound and cement taxonomic errors. These revisions

are also greatly influenced by the current state of taxonomy in the general literature, which is often grounded on smaller revisions that can overreach with the purported understanding of wider internal infra-familial relationships.

METHODOLOGY FOR DISCERNING PHYLOGENY

Pure cladistics searches are the most parsimonious hierarchical arrangements based on character scoring of terminal taxa that do not include evolutionary considerations, nor the geographical distribution of the characters used (Davis and Nixon 1992). Thus, cladistical hierarchy is purely an epistemological axiom that is without an explanatory causal hypothesis (Brower 2000). In contrast, phylogenetics is a form of cladistics that seeks to reconstruct relationships that are dependent on the distribution of characters (Davis and Nixon 1992). In order to achieve this, species must be treated as separate terminals (Yeates 1995). In creating terminals, the taxonomist is then able to either intuitively deduce ground plan character states of the higher clades, or choose exemplars that represent real species, both of which have the same goal of providing the basis for coding (Yeates 1995). The discovery of islands of individuals within multiple most parsimonious trees enables the determination of these exemplars (Maddison 1991). Definitions should only be applied to clades after considered analysis and a sound basis for need has been established, particularly with reference to the delineation of islands out of greater diverse organism character set (Brochu and Samrall 2001). This need is systematically subjective and may be argued on a basis of phylogenetic support, phenotypic distinctiveness, ecological significance, economic importance or some other argument made by the taxonomist (Forey 2002). However, it is a phylogenetic principle that the formation of the definition of higher

taxa has stability and that there is unambiguous interpretation of what taxa are to be included and excluded. That is, uses of the name in association with a particular key stone taxon, represented by a type, must have priority (de Queiroz and Gauthier 1990).

Two forms of evidence were used to generate phylogenies for West African and American Strombidae. The cytochrome oxidase I (COI) mitochondrial subunit evidence comprised the first data set derived from Latiolais *et al.* (2006). Anatomical character states from Simone (2005) formed a second set of data. The results of this analysis were examined within the context of Bandel's (2007) and Dekkers' (2008a, 2008b) hypothetical relationships.

Molecular Information

We revisited molecular data and generated new phylogenies to confirm hypothetical relationships postulated in Latiolais *et al.* (2006). Eleven COI sequences were obtained from GenBank: DQ525222 *Strombus gigas* Linné, 1758 (= *Eustrombus gigas* (Linné, 1758)) (Latiolais *et al.* 2006); DQ525223 *Strombus granulatus* Swainson, 1822 (= *Persististrombus granulatus* (Swainson, 1822)) (Latiolais *et al.* 2006); DQ525224 *Strombus latus* Gmelin, 1791 (= *Thetystrombus latus* (Gmelin, 1791)) (Latiolais *et al.* 2006); DQ525227 *Strombus peruvianus* Swainson, 1823 (= *Lobatus peruvianus* (Swainson, 1823)) (Latiolais *et al.* 2006); DQ525226 *Strombus raninus* Gmelin, 1791 (= *Lobatus raninus* (Gmelin, 1791)) (Latiolais *et al.* 2006); DQ525225 *Strombus costatus* Gmelin, 1791 (= *Macrostrombus costatus* (Gmelin, 1791)) (Latiolais *et al.* 2006); DQ525221 *Strombus gallus* Linné, 1758 (= *Aliger gallus* (Linné, 1758)) (Latiolais *et al.* 2006); DQ525220 *Strombus galeatus* Swainson, 1823 (= *Titanostrombus galeatus* (Swainson, 1823)) (Latiolais *et al.* 2006); DQ525209

Strombus gracilior Sowerby, 1825 (Latiolais *et al.* 2006); DQ525208 *Strombus alatus* Gmelin, 1791 (Latiolais *et al.* 2006); and DQ525207 *Strombus pugilis* Linné, 1758 (Latiolais *et al.* 2006). Sequences were aligned prior to analysis using CLUSTALW fast pairwise alignment and checked visually (Larkin *et al.* 2007). No gaps were opened in the sequences during alignment.

Molecular data were entered into MEGA X (Kumaer *et al.* 2018; Saitou and Nei 1987; Rzhetsky and Nei 1992). All trees generated were tested using 50 bootstrap replicates, the level of bootstrapping reflects the data matrix size and lack of gaps in alignment. Where multiple trees were generated, only the consensus tree is presented unless any divergence indicated a significant cladistic anomaly from another tree. Two forms of analysis were undertaken: Maximum Likelihood evolutionary history was inferred based on the Jukes-Cantor model (Jukes and Cantor 1969) and the Unweighted Pair Group Method with Arithmetic Mean (UPGMA; Sneath and Sokal, 1973), with the base assumption of a uniform rate of evolution under the Jukes-Cantor model (Nei and Kumar 2000). The ability to choose the evolutionary model overcomes many of the black box issues associated with earlier models of the MEGA software.

Anatomical Information

Simone (2005) provided a seminal overview of the anatomy of American Strombidae Rafinesque, 1815, and the anatomical characters for eight taxa were derived from that work and used in this review: *Aliger costatus* (Gmelin, 1791) (= *Macrostrombus costatus* (Gmelin, 1791)); *Aliger gallus* (Linné, 1758); *Aliger gigas* (Linné, 1758); *Eustrombus goliath* (Schröter, 1805) (= *Titanostrombus goliath* (Schröter, 1805)); *Strombus alatus* Gmelin,

1791; *Strombus gracilior* Sowerby, 1825; *Strombus pugilis* Linné, 1758; and *Tricornis raninus* (Gmelin, 1791)(= *Lobatus raninus* (Gmelin, 1791)). Fourteen characters were utilized and coded for, and these represented differences in the anatomy of the reproductive system, buccal structure, kidneys, mantle and the organs within the cavity formed by it, and body dorsal surface textures (Table 2). Analyses of anatomical characters coded for were conducted in MEGA X (Kumaer *et al.* 2018). Trees were generated using Maximum Likelihood with a neutral evolutionary model. Character states were transcribed and coded (1 = A, 2 = G, 3 = C, 4 = T) to represent states. Maximum Likelihood evolutionary history was inferred based on the Jukes-Cantor model (Jukes and Cantor 1969). All trees generated were tested using 50 bootstrap replications, which is reflective of the data matrix size. This novel approach of using software developed for molecular analysis for character states was tested using anatomical characters against known trees that were generated with traditional software and using the same character sets and indicates no difference in internal relationships (Simone 2005).

RESULTS

Molecular Analyses

The maximum likelihood analysis of the COI data produced one tree with log likelihood of -3152.21 (Figure 2B). The tree generated during this retesting conformed completely to Latiolais *et al.*'s (2006) COI and H3 combined maximum likelihood gene tree (Figure 1A). The UMPGA analysis resulted in a COI gene consensus tree similar in overall branch structure and internal resolution presented by Latiolais *et al.*'s (2006) COI and Histone 3 (H3) combined maximum likelihood gene tree (Figure 2A). However, there were some differences between the two

trees. First the positioning of *Lentigo* Jousseaume, 1886 (= *Persististrombus* Kronenberg and Lee, 2007; = *Thetystrombus* Dekkers, 2008) was paraphyletic in Latiolais *et al.* (2006) but is presented as the sister taxon to *Persististrombus* Kronenberg and Lee, 2007 and *Thetystrombus* Dekkers, 2008 in this analysis. Another difference is the treatment of the internal content of the Latiolais *et al.* (2006) clade *Tricornis* Jousseaume, 1886 which is currently restricted to the extant Indo-Pacific. The position of *Titanostrombus* Petuch, 1994 in relation to its sister taxon remains unclear, and its position within the phylogeny is dependent on the phylogenetic methodology used (Figure 2A, B). However, results indicate a sister taxa relationship between *Macrostrombus* Petuch, 1994, *Aliger* Thiele, 1929 and *Titanostrombus* Petuch, 1994.

Anatomical Analysis

There was no difference between the tree generated using anatomical data analysed with Mega X and that illustrated by Simone (2005) generated using more conventional cladistic programmes (cf. Figure 1B and 2C). The anatomical maximum likelihood analysis produced one tree with log likelihood of -84.77. Cladistic analysis of the anatomical evidence indicated two distinct clades. The first contained *Strombus* Linné, 1758 and this formed Simone's (2005) unidentified clade 15. The second clade, clade 16 in Simone (2005), is more complex and is represented by the *Aligerina* nov. subtribus, and is divided between: 1) *Macrostrombus* Petuch, 1994, *Lobatus* Iredale, 1921, and *Aliger* Thiele, 1929 which Simone (2005) identified as clade 18; and 2) the Simone (2005) clade 17 containing both *Titanostrombus* Petuch, 1994 and *Aliger* Thiele, 1929.

OVERVIEW OF SYSTEMATICS

Historically, the Western Atlantic and Eastern Pacific (Panamic) stromboid species, including *Thetystrombus latus* Gmelin, 1791 from West Africa were considered monophyletic and derived from a single radiation event (Clench and Abbott 1941; Kronenberg and Vermeij 2002). Kronenberg and Lee (2007) proposed several theories to explain radiation of American stromboids. The first accepted theory is premised on the *Persististrombus* Kronenberg and Lee, 2007 arriving in one or two waves: one resulting in *Strombus* Linné, 1758 and the other accounting for all the remaining stromboids species (Kronenberg and Lee 2007). The second theory, while rejected by Kronenberg and Lee (2007), is premised on a common ancestry derived out of *Dilatilabrum* Cossmann, 1904 from the Lutetian (Middle Eocene) of Italy based on the widely extended outer lip. Purportedly, the line terminated with the Oligocene *Dilatilabrum roegli* Harzhauser, 2001. However, the placement of this taxon within *Dilatilabrum* Cossmann, 1904 needs review. The third theory also rejected by Kronenberg and Lee (2007) is grounded in Beneventi and Piccoli (1969) and Sacco (1893), where a relationship exists between American and European stromboids through the *Strombus* (s.l.) *coronatus* (Defrance, 1827) complex, which is the possible ancestor of *Thetystrombus* Dekkers, 2008. We reject all these hypotheses and argue that the radiation occurred twice at different times and from different lineages.

Furthermore, this paper addressed both the irregularities in American stromboid taxonomy. This was achieved through the use of total evidence, which brings previous revisions that used different methodological approaches together, to generate a phylogeny that illustrates the relationships between extant members of the Strombidae (Figure 3). Two clades that were

resolved here have not been identified previously, and we suggest that these represent the possible independent ancestral incursions into the Americas: *Aligerini nov. tribus* and *Persististrombini nov. tribus*. The *Persististrombini nov. tribus* includes two clades at the generic level, *Thetystrombus* Dekkers, 2008 and *Persististrombus* Kronenberg and Lee, 2007. *Thetystrombus* Dekkers, 2008 is postulated to have arisen out of a common ancestor shared with *Persististrombus* Kronenberg and Lee, 2007 (Dekkers 2008a; Harzhauser and Kronenberg 2013). This occurred during the upper Paleogene. Furthermore, the varying placement of these two clades in relation to other taxa indicates they have different evolutionary trajectories. The limitation on inclusivity within this paper makes drawing conclusions on the basal relationships between these clades problematic. This is because there is no ancestral context relative to the wider familial group outside of the defined taxa. However, the fossil records indicate a divergence between the *Persististrombini nov. tribus* and the *Aligerini nov. tribus* occurring within the upper Paleogene (Dall 1890; Petuch 2004).

Based on the distribution of the fossil records, the remaining American Strombidae Rafinesque, 1815 are not all related to *Persististrombus granulatus* Swainson, 1822, but fall into the natural clade *Aligerini nov. tribus*. Given that there is no definitively resolved outgroup to provide ancestral grounding within this study, the most appropriate definition is nodal in form. *Aligerina nov. subtribus* forms a monophyletic, enclosed and definable clade that is robustly divided into two sub-clades namely the stem clade *Strombus* Linné, 1758; and the nodal clade containing *Aligerina nov. subtribus*. These two clades represent robust clades that have evolved defining anatomical and morphological characters that enable clear delineation.

However, both share a pre-Miocene common ancestry, and we hypothesize that both are derived from a single and independent colonising event giving rise first to *Edpetuchistrombus nov. gen.* and then *Antestrombus nov. gen.* in the early Miocene of Florida.

The erection of *Aligerina nov. subtribus* represents the point of a common ancestry between *Edpetuchistrombus nov. gen.* and *Antestrombus nov. gen.*. The fossil record indicates however, that there has been a long period of divergence between these two taxa (Petuch 1994). *Lobatus* Iredale, 1921 and its *Aligerina nov. subtribus* sister crown clade share some unifying morphological characteristics, such as the tendency for distinctive uniform ribbing dorsally, the somewhat flaring lip, and the lack of sculpture within the aperture. The extant remaining members of these groups are represented by a limited number of taxa. However, each represents a greater number of fossil taxa, such that the extant taxa represent only the tip of an historical extinction iceberg. Nomenclatural significance of these taxa should not be governed only on criteria that seeks to avoid monotypicity in extant taxa. The reduction of higher taxonomic relationships based, in part, on hybridization fails to understand that successful mating can occur between genetically dissimilar organisms (Soltis and Soltis 2009). This taxonomic collapse limits the ability to construct a phylogeny that assists in explaining evolutionary theory.

The clade *Strombus* Linné, 1758 is well resolved out of the more inclusive Strombidae Rafinesque, 1815, with a diverse and rich fossil history arising out of the Miocene Lower Gatun *Edpetuchistrombus aldrichi* (Dall, 1890) complex. Practically, there is no explanatory advantage in erecting the subtribe to include

only *Strombus* Linné, 1758 as the definition of the clades is evolutionarily explicit and can be compared with taxa at any level.

Edpetuchistrombus nov. gen. is erected to encapsulate the lower Miocene Chipola River taxa that are directly related to *Edpetuchistrombus aldrichi* (Dall, 1890) that arrived between the Oligocene to very Early Miocene from Europe. *Strombus* (s.l.) *liocyclus* Dall, 1915, a very rare species from the Tampa Silex beds, Florida, most likely of Late Oligocene beds, is also one of the early intruders, and its placement is uncertain.

The extant *Strombus* Linné, 1758 have generally smooth body whorls except for the sometimes-strong knobs (or even spine-like knobs) and some axial growth lines. There is a general difference in form between *Edpetuchistrombus* nov. gen., which tends towards being ovate, and the biconic form of *Antestrombus* nov. gen.. *Antestrombus* nov. gen. is herein erected to encapsulate the lower Miocene (Burdigalien) Chipola River species related to *Antestrombus chipolanus* (Dall, 1890) and *Antestrombus mardieae* (Petuch, 2004). With the erection of *Edpetuchistrombus* nov. gen. and *Antestrombus* nov. gen., we hypothesise that the Miocene *Edpetuchistrombus aldrichi* (Dall, 1890) and *Antestrombus chipolanus* (Dall, 1890) complexes represent the split and transition towards *Aligerina* nov. subtribus and *Strombus* Linné, 1758. Notwithstanding, this paper argues that there were two waves, the first bringing the *Persististrombini* nov. tribus and the second wave bringing the *Tersusini* nov. tribus.

The clade *Pyramis* Röding, 1798 (Type *Strombus lucifer* Linné, 1758 = *Strombus gigas* Linné, 1758) is herein not considered taxonomically sound. The internal content of the clade indicates that Röding (1798) may have

intended this to contain juveniles of many families, that prior to reaching terminal growth, have remarkable growth similarity in shape and lip structure, and not to describe the Strombidae Rafinesque, 1815 members that are clearly placed in *Lambis* Röding, 1798.

The use of types to define basal taxa avoids paraphyletic genera as they are independent terminals of the tree. As a result of the internal resolution of the phylogeny of the American Strombidae, the genus *Lobatus* Swainson, 1837 is limited to the extant *Lobatus raninus* (Gmelin, 1791) and several fossil precursors. The genera *Macrostrombus* Wenz, 1940, *Aliger* Thiele, 1929 and *Titanostrombus* Petuch, 1994 are reinstalled as valid genera. The genus *Persististrombus* Kronenberg and Lee, 2007, which was used as a pit for a plethora of species, is now limited to the extant *Persististrombus granulatus* (Swainson, 1822), fossil American species and a few Oligocene to Miocene Indo-European species. Two new genera for the Miocene ancestral basal taxa of *Aligerini* nov. tribus, *Edpetuchistrombus* nov. gen. and *Antestrombus* nov. gen., are proposed, both of which represent basal reference points, enabling greater clarity in the resolution of early West African and American Strombidae Rafinesque, 1815.

SYSTEMATICS

Phylum	Mollusca Linné, 1758
Superorder	Caenogastropoda Cuvier, 1797
Order	Sorbeoconcha Ponder & Lindberg, 1987
Superfamily	Stromboidea Rafinesque, 1815
Epifamily	Neostromboidae Maxwell, Dekkers, Rymer & Congdon, 2019
Family	Strombidae Rafinesque, 1815

Persististrombini nov. tribus

Type. *Persististrombus* Kronenberg and Lee, 2007 (Type: *Strombus granulatus* Swainson, 1822).

Definition. Contains all recent taxa of the most common ancestors shared between *Persististrombus* Kronenberg and Lee, 2007 and *Thetystrombus* Dekkers, 2008, and does not include those ancestors more closely related to *Aligerini nov. tribus*.

Diagnosis. A small to medium sized shell with a thin edged outer lip that may be lightly calloused in part. The outer lip is not expanded, and attaches at the shoulder of the body whorl. The sculpture of the aperture wall is variable, ranging from smooth to granulate. The columella is smooth and calloused anteriorly. The basal sinus is well developed. Shell sculpture with shoulder knobs.

Etymology. Formed with reference to the type genus *Persististrombus* Kronenberg and Lee, 2007.

***Persististrombus* Kronenberg & Lee, 2007**

Type species. *Strombus granulatus* Swainson, 1822.

Definition. All members more closely related to *Persististrombus granulatus* (Swainson, 1822) and the clade bound by it.

Synonymy. *Persististrombus* Kronenberg and Lee, 2007, p. 257

Original Diagnosis. “Shell of moderate size for family, fusiform, shoulder knobs distinct on body whorl, slightly expanded outer lip with sharp, unglazed rim and no extensions, regularly divided callus on columella, anterior canal short, posterior canal or groove absent or obsolete. Protoconch elongate and conical with four to five smooth whorls. Adaxial side of outer lip smooth, plicate, or granulate” (Kronenberg and Lee 2007, p. 257).

Description. The shell with a sharp outer lip, anteriorly strongly quadrate and not axially reflected. The inner lip is granulated or lirate. The mid-body whorl with rows of nodules. The shell is solid and heavy, with an anterior canal that is reflected.

Assigned Taxa: *Strombus baltrae* Garcia-Talavera, 1993 [Pliocene, Galapagos, Ecuador], *Strombus (Lentigo) barrigonensis* Jung & Heitz, 2001 [Early Pliocene, Venezuela], *Strombus granulatus* Swainson, 1821 [Pliocene to Recent, tropical eastern Pacific] (Figure 4A), *Strombus (Lentigo) insulanus* Jung & Heitz, 2001 [Middle Pliocene, Caribbean Panama], *Mitra nodosa* Borson, 1820 [Lower Miocene, Italy], *Strombus bonelli* Brongniart, 1823 [Lower Miocene, Italy], *Strombus obliterated* Hanna, 1926 [Pliocene, California, USA], *Strombus praecedens* Schaffer, 1912 [Lower Miocene, Austria], *Pterocerus radix* Brongniart, 1823 [Lower Oligocene, Italy], *Strombus (lentigo) toroensis* Jung & Heitz, 2001 [Early Pliocene, Panama].

***Thetystrombus* Dekkers, 2008**

Type species. *Strombus latus* Gmelin, 1791.

Definition. All taxa more closely related to *Thetystrombus latus* (Gmelin, 1791) and the clade bound by it, than to *Persististrombus* Kronenberg and Lee, 2007.

Synonymy. *Afristrombus* Bandel, 2007, p. 143 (Type: *Strombus latus* Gmelin, 1791).

Original Diagnosis. “Shell large to very large, solid but mostly thin walled, light to medium weight shells. The form of the shell is ovoid. Outer lip has a striking thin end which characterizes the genus. Body whorl decorated with knobs on the shoulder, sometimes nearly smooth and sometimes large to very large knobs reflecting to spines. Stromboidal notch is present, mostly large. The base left of the canal is rounded and smooth, no finger like small projections. The sculpture of the body whorl is

besides the aforementioned knobs rather smooth and consists merely of small growth line. The inside of the lip is smooth, just as the columella” (Dekkers 2008, p. 55).

Description. The shell with an outer lip that is centrally calloused and not axially reflected; teleoconch with regular nodulations; inner lip smooth; body whorl without striae; shell thin and light; and the anterior canal is straight.

Assigned Taxa: *Strombus coronatus* (Defrance, 1827) [Pliocene, Italy etc.], *Strombus exbonellii* Sacco, 1893 [Middle Miocene, Austria], *Strombus inflexus* Eichwald, 1830 [Middle Miocene, Ukraine], *Strombus lapugyensis* Sacco, 1893 [Middle Miocene, Hungary], *Strombus latus* Gmelin, 1791 [Pleistocene – Recent, Mediterranean – West Africa] (Figure 4B), *Persististrombus panonicus* Harzhauser & Kronenberg, 2013 [Middle Miocene, Austria].

Aligerini nov. tribus

Type. *Aliger* Thiele, 1929 (Type: *Strombus gallus* Linné, 1758).

Definition. Contains all recent taxa of the most common ancestor between *Strombus* Linné, 1758 and *Aligerina nov. subtribus* and does not include those ancestors more closely related to *Persististrombini nov. tribus*.

Diagnosis. The shell is solid, heavy, with a smooth and calloused outer lip. The body whorl is smooth or with uniform axial sculpture. The basal sinus is variable in depth.

Etymology. Derived from the subordinate genus *Aliger* Thiele, 1929.

Aligerina nov. subtribus

Type. *Aliger* Thiele, 1929 (Type species: *Strombus gallus* Linné, 1758).

Definition. Contains all members of the *Aligerini nov. tribus* that are not encapsulated within *Strombus* Linné, 1758.

Diagnosis. The shell is heavy and moderately large with a broad outer lip that is calloused and thickened. The basal sinus is present.

Etymology. Derived from the subordinate genus *Aliger* Thiele, 1929.

Aliger Thiele, 1929

Type species. *Strombus gallus* Linné, 1758.

Definition. Contains all recent members of the *Aligerina nov. subtribus* that are not encapsulated within *Macrostrombus* Petuch, 1994, *Titanostrombus* Petuch, 1994 or *Lobatus* Iredale, 1921.

Synonymy. *Strombus (Aliger)* Thiele, 1929, p. 254; *Eustrombus* Wenz, 1940, p. 945 (Type: *Strombus gigas* Linné, 1758) [Note: A uninominal name proposed for a genus-group division of a genus, even if proposed for a secondary (or further) subdivision, is deemed to be a subgeneric name even if the division is denoted by a term such as “section” or “division”; but a name used for an aggregate of species, which is denoted by a term such as “superspecies”, is not deemed to be a genus-group name (ICZN 1999, art. 6.2)]

Original Diagnosis. “Schale mit starken Knoten und Spiralreifen, Mundrand bedeutend erweitert und oben einen splitzen Flügel bildend” (Thiele 1929, p. 254). Shell with strong knobs and spiral ribbing, apertural rim rather broad and on the upper part winged and pointed. (Translation AMD)

Description. The shell outer lip is inflated, with widely, expanded, uniformly thickened lips as adults, but is not axially reflected; posterior end of lip narrowing to projection or point, giving the aperture a triangulate shape; shoulders often ornamented with large knobs; shell moderately heavy and solid; and an anterior canal that is reflected.

Assigned Taxa: *Strombus dominator* Pilsbry & Johnson, 1917 [upper Miocene-lower Pliocene, Dominican Republic], *Strombus galliformis*

Pilsbry & Johnson, 1917 [Pliocene, Dominican Republic], *Strombus gallus* Linné, 1758 [Pleistocene – Recent, Caribbean] (Figure 5A), *Strombus gigas* Linné, 1758 [Pleistocene–Recent, Caribbean] (Figure 5B).

***Lobatus* Iredale, 1921**

Type species. *Strombus bituberculatus* Lamarck, 1822 (= *Lobatus raninus* (Gmelin, 1791)).

Definition. Contains all recent members of the *Aligerina* nov. subtribus that are not encapsulated within *Macrostrombus* Petuch, 1994, *Titanostrombus* Petuch, 1994 and *Aliger* Thiele, 1929.

Synonymy. *Lobatus* Swainson ex Iredale, 1921, p. 208.

Original Diagnosis. Iredale provides a scant reference to a purported Swainson (1837) manuscript where the remark *Lobatus* is inserted next to *Strombus bituberculatus* Lamarck, 1822. “Only three names appear to be of importance: thus on p. 67, under the genus *Turbinella*, against a series beginning with *T. capitellum*, there is noted in brackets *Plicatella*, Swainson, and on p. 75, in the same manner, *Lobatus*, Swainson, is recorded for *Strombus bituberculatus*; and on p. 81. *Buccinulum*, Swainson is referred to in connection with *Buccinum lineatum*, *lineolatum*, *maculosum* and *coromandelianum*” (Iredale 1921: p.208).

Description. The shell is triangulate, heavy and solid; outer lip axially reflected and posteriorly tricornate with uniform callosity; mid-dorsal body whorl with striae and rows of nodules; and the anterior canal is reflected.

Assigned Taxa: *Strombus peruvianus* Swainson, 1823 [Pleistocene–Recent, tropical eastern Pacific] (Figure 5C), *Strombus raninus* Gmelin, 1791 [Pleistocene–Recent, Caribbean] (Figure 5D).

***Macrostrombus* Petuch, 1994**

Type species. *Strombus costatus* Gmelin, 1791.

Definition. Contains all recent members of the *Aligerina* nov. subtribus that are not encapsulated within *Aliger* Thiele, 1929, *Titanostrombus* Petuch, 1994 or *Lobatus* Iredale, 1921.

Synonymy. *Macrostrombus* Petuch, 1994, p. 258.

Original Diagnosis. “*Strombus* shells that are much larger than *Strombus* s.s., massive, inflated, with widely, expanded, thickened lips as adults; posterior end of lip rounded, not narrowing to projection or point; body whorls sculptured with large flattened cords, giving shells ribbed appearance; shoulders often ornamented with large spike-like knobs” (Petuch 1994: p. 258). [Comment – Petuch (1994, p. 258): “This endemic western Atlantic strombid radiation, which appears to have been centred on the Floridian Peninsula, has traditionally been placed in the subgenus *Eustrombus* Wenz, 1940 (type: *S. gigas* Linnaeus, 1758) (note: Abbott (1960) incorrectly placed *S. gigas* in *Tricornis* Jousseaume, 1886 - an unrelated, endemic Indo-Pacific, Red Sea subgenus). Since members of *Macrostrombus*, although large like *Eustrombus*, lack the large shoulder spikes of the *S. gigas* complex, have heavily-ribbed body whorl sculptures, and have more rounded, non-projecting lips, I felt it necessary to erect a separate subgenus for this compact western Atlantic group.”]

Description. The shell dorsum with uniform striae; teleoconch whorls knobbed; body whorl with shoulder nodulations; outer lip centrally calloused, posteriorly quadrate and thinned; outer lip edge axially reflected with glazing; aperture smooth; shell heavy and solid and an anterior canal that is reflected.

Assigned Taxa: *Macrostrombus bartoni* Petuch & Drolshagen, 2011 [Plio-Pleistocene,

Florida, USA], *Strombus* (*Macrostrombus*) *brachior* Petuch, 1994 [lower Pleistocene, Florida, USA], *Macrostrombus briani* Petuch & Drolshagen, 2011 [Pliocene, Florida, USA], *Macrostrombus collierensis* Petuch & Drolshagen, 2011 [Pliocene, Florida, USA], *Strombus costatus* Gmelin, 1791 [Pleistocene – Recent, Florida, Caribbean] (Figure 5E), *Strombus diegelae* Petuch, 1991 [middle Pleistocene, Florida, USA], *Macrostrombus dubari* Petuch & Drolshagen, 2011 [Pleistocene, Florida, USA], *Strombus haitensis* Sowerby, 1850 [Miocene, Dominican Republic], *Strombus* (*Eustrombus*) *hertweckorum* Petuch, 1991 [Pliocene, Florida, USA], *Strombus jonesorum* Petuch, 1994 [Pleistocene, Florida, USA], *Strombus leidy* Heilprin, 1887 [upper Pliocene, Florida, USA], *Strombus mayacensis* Tucker & Wilson, 1933 [Pliocene, Florida, USA], *Strombus* (*Macrostrombus*) *mayacensis holeylandicus* Petuch, 1994 [Pleistocene, Florida, USA], *Strombus mulepenensis* Petuch, 1994 [Pliocene, Florida, USA], *Macrostrombus oleiniki* Petuch & Drolshagen, 2011 [Pleistocene, Florida, USA], *Lobatus pascaleae* Landau, Kronenberg & Silva, 2010 [Late Miocene, Dominican Republic], *Macrostrombus sargenti* Petuch & Drolshagen, 2011 [Pleistocene, Florida, USA], *Macrostrombus tomeui* Petuch & Drolshagen, 2011 [Pleistocene, Florida, USA], *Strombus williamsi* Olsson & Petit, 1964 [Late Pliocene, Florida, USA], *Macrostrombus whicheri* Petuch & Drolshagen, 2011 [Pleistocene, Florida, USA].

Edpetuchistrombus nov. gen.

Type species. *Strombus aldrichi* Dall, 1890.

Definition. Contains all ancestral members of *Aligerini* nov. tribus more closely related to *Aligerina* nov. subtribus than to *Strombus* Linné, 1758.

Diagnosis. Shells of moderate size; ovate; spire with spiral lines and knobs; body whorls with evenly spaced spiral ribbing that run also on the relatively large shoulder knobs; lip flaring, aperture straight, not glazed within; aperture extends posteriorly before the pre-ultimate whorl. The spiral ribbing runs over the extended lip, bending backwards. Apertural rim not glazed. The anterior canal not broad and a little reflected to the left. The Stromboid notch is present but shallow.

Etymology. The name *Edpetuchistrombus* nov. gen. is chosen in honour of Edward J. Petuch, Florida, USA, for the inspiring work he has done on extant and fossil molluscs in Florida and the Caribbean and especially the research on Strombidae species and genera, with his ground-breaking ideas on the seas and sub-seas and the formations from the Miocene to present.

Assigned Taxa: *Strombus aldrichi* Dall, 1890 [Lower Miocene, Florida, USA] (Figure 6A).

Titanostrombus Petuch, 1994

Type species. *Strombus goliath* Schröter, 1805.

Definition. Contains all recent members of the *Aligerina* nov. subtribus that are not encapsulated within *Aliger* Thiele, 1929, *Macrostrombus* Petuch, 1994 or *Lobatus* Iredale, 1921.

Synonymy. *Titanostrombus* Petuch, 1994, p. 261.

Original Diagnosis. “*Strombus* shells that reach the largest sizes for the family, massive, inflated, with uniformly thin, expanded lips as adults; posterior end of lip rounded; body whorls sculptured with wide, closely-packed, flattened ribs; spire whorls low and generally flattened; spire whorls often with large spike-like knobs; knobs become obsolete on body whorl; body whorl rounded, without spikes or knobs; shoulder rounded, often with faint axial undulations” (Petuch, 1994: p. 261). [Comment – Petuch (1994, p. 261): “This group

of giant strombids is unique to the tropical Americas, with a living species in both the Eastern Pacific and western Atlantic (Brazil). The only known fossil species, *S. williamsi* (Plate 20, Figure A) is found only in the Holey Land Fauna of the Everglades region, and is known from fewer than a dozen specimens. While *S. (Titanostrombus) goliath* is the largest living species, *S. (Titanostrombus) williamsi* is the largest-known fossil strombid (with specimens in excess of 300 mm). *Titanostrombus* is similar to *Macrostrombus*, but differs in being consistently larger, in having more rounded shoulders, and in having large, spikelike knobs on the early whorls. In this last character, *Titanostrombus* is similar to *Eustrombus* (type *S. gigas*). The co-occurrence of three giant strombid genera, *Macrostrombus*, *Eustrombus*, and *Titanostrombus*, together in southern Florida during Holey Land time, is truly remarkable".]

Description. The shell outer lip is uniformly thin on the border, thickened centrally, expanded and rounded posteriorly; body whorl sculptured with broad narrow interspaced ribs; teleoconch often with large knobs; knobs become obsolete on body whorl; shell moderately heavy and solid; and an anterior canal that is reflected.

Assigned Taxa: *Titanostrombus immokaleensis* Petuch & Drolshagen, 2011 [Pliocene, Florida, USA], *Strombus galeatus* Swainson, 1823 [Pleistocene – Recent, tropical East Pacific] (Figure 5F), *Strombus goliath* Schröter, 1805 [Recent, Brazil] (Figure 5G).

Strombina nov. subtribus

Type. *Strombus* Linné, 1758 (*Strombus pugilis* Linné, 1758 by subsequent designation Lamarck (1799)).

Definition. Contains all recent members of the *Aligerini nov. tribus* that are not encapsulated within *Aligerina nov. subtribus*.

Diagnosis. Shells biconic with the apertural rim not glazed. The edge of lip somewhat thickened posteriorly and calloused, becoming thinner and sharper anteriorly.

Etymology. Derived from subordinate genus *Strombus* Linné, 1758.

Antestrombus nov. gen.

Type species. *Strombus chipolanus* Dall, 1890.

Definition. Contains all ancestral members of the clade *Strombini nov. tribus* more closely related to *Strombus* Linné, 1758 than to *Aligerina nov. subtribus*.

Diagnosis. Shells of moderate size. Spire acute, with spiral lines and axially aligned knobs. Body whorl reversed conoidal form. The body whorl has evenly spaced spiral ribbing that is almost smooth, with relatively large and sharp shoulder knobs. The non-flaring lip with a straight side. The aperture large but narrow and not extending posteriorly before the body whorl. The spiral ribbing runs over the extended lip and bends slightly backwards at the posterior end. The apertural rim not glazed but a little thickened by shell material added from the inside of the aperture. Inside outer lip smooth. The anterior canal not broad, but deep, and slightly reflected to the left. Stromboid notch present but shallow.

Etymology. The name *Antestrombus nov. gen.* is chosen to indicate the close resemblance with fossil and extant species of the genus *Strombus* Linné, 1758. The prefix *ante* is indicative that species belonging to the new genus are precursors of a plethora of species that evolved and thrived in the Plio-Pleistocene of Florida and the Caribbean Seas.

Assigned Taxa: *Strombus chipolanus* Dall, 1890 [lower Miocene, Florida, USA] (Figure 6 B), *Strombus dodoneus* Gardner, 1947 [Late Miocene, Florida, USA], *Strombus mardieae* Petuch, 2004 [lower Miocene, Florida, USA] (Figure 6 C). Note: *Strombus dodaneus* Gardner,

1947 is bridging between *Antestrombus* nov. gen. and *Strombus* Linné, 1758.

***Strombus* Linné, 1758**

Type species. *Strombus pugilis* Linné, 1758 by subsequent designation Lamarck (1799).

Definition. Contains all recent members of the *Aligerini* nov. tribus that are not encapsulated within subtribe *Aligerina* nov. subtribus.

Synonymy.

Strombus Linné, 1758, p. 742;

Strombella Schlüter, 1838, p. 22 (Type: *Strombus pugilis* Linné, 1758);

Pyramis Röding, 1798 (Type: *Pyramis striata* Röding, 1798 = *Strombus pugilis* Linné, 1758).

Description. The shell triangulate to fusiform, medium in size, The columella smooth, and the outer-lip strongly axially quadrate posteriorly. The edge of the lip somewhat thickened posteriorly and calloused, becoming thinner and sharper anteriorly. The shoulder with nodules, and the body whorl is smooth or with fine axial uniform striations. The outer aperture smooth, or with fine short lirations.

Assigned Taxa: *Strombus acanthospira* Landau, Kronenberg, Herbert & Silva, 2011 [Calabrian: Pleistocene, Panama], *Strombus alatus* Gmelin, 1791 [Pleistocene - Recent, Florida & Caribbean] (Figure C), *Strombus arayaensis* Landau and Silva, 2010 [Pleistocene, Venezuela], *Strombus ayersensis* Petuch & Drolshagen, 2011 [Pleistocene, Florida, USA], *Strombus bifrons* Sowerby, 1850 [Late Miocene, Dominican Republic], *Strombus capelettii* Petuch, 1994 [Middle Pleistocene, Florida, USA], *Strombus cannoni* Petuch & Drolshagen, 2011 [Pliocene, USA], *Strombus elegantissimus* Landau, Kronenberg, Herbert & Silva, 2011 [Late Pliocene, Panama], *Strombus erici* Petuch, 1994 [Calabrian Pleistocene, USA], *Strombus evergladesensis* Petuch, 1991 [Pleistocene, USA], *Strombus floridanus* Mansfield, 1930

[Upper Miocene, USA], *Strombus gatunensis* Toula, 1909 [Miocene, Panama], *Strombus gracilior* Sowerby, 1825 [Recent, Eastern Pacific] (Figure 4D), *Strombus jenniferae* Petuch & Drolshagen, 2011 [Pleistocene, USA], *Strombus keatonorum* Petuch, 1994 [Lower Pleistocene, Florida, USA], *Strombus leurus* Woodring, 1928 [Pliocene, Jamaica], *Strombus lindae* Petuch, 1991 [Pleistocene, USA], *Strombus propegracilior* Dall & Ochsner, 1928 [Pliocene, Galapagos], *Strombus proximus* Sowerby, 1850 [Miocene, Dominican Republic], *Strombus pugilis* Linné, 1758 [Recent, Caribbean] (Figure 4E). *Strombus pugiloides* Guppy, 1873 [Pliocene, Jamaica], *Strombus sarasotaensis* Petuch, 1994 [Pliocene, USA], *Strombus subgracilior* Durham, 1950 [Middle and Upper Pliocene], *Strombus vermeiji* Landau, Kronenberg, Herbert & Silva, 2011 [Neogene, Panama], *Strombus worki* Petuch, 1983 [Recent, Brazil] (Figure 4F).

DISCUSSION

One of the most significant problems in bringing an evolutionary understanding to the nomenclature is the blurring of ancestral relationships through overreach within the census literature in attribution to *Persististrombus* Kronenberg and Lee, 2007. The blurring of ancestral relationships through the oversimplification of the higher taxonomy has decreased the contribution that these genera can make to the evolutionary understanding of taxonomic radiations on a global scale (Dekkers 2008b). Lozouet and Meaestrati (1986) demonstrated the link between the European Early Oligocene *Persististrombus radix* (Brongniart, 1823) (France, Aquitaine Basin) and the extant *Persististrombus granulatus* (Swainson, 1822). The overreach of the consensus in definable inclusivity within *Persististrombus* Kronenberg and Lee, 2007 has had the negative side effect of creating a level of

taxonomic inflation, where the increase in attributed taxa with more diverse morphology indirectly expands the accepted character set, and where the importance of the inclusivity within the genus appears to override the original description. The genus *Persististrombus* Kronenberg and Lee, 2007 is herein restricted to the American species: *P. granulatus* (Swainson 1822), *P. barrigonensis* (Jung and Heitz, 2001), *P. toroensis* (Jung and Heitz, 2001), *P. insulanus* (Jung and Heitz, 2001), *P. obliterated* (Hanna, 1926) and *P. baltrae* (Garcia-Talavera, 1993). Kronenberg and Lee (2007) included ancestral species that fall outside the defining characteristics of that clade *Persististrombus* Kronenberg and Lee, 2007, such as *Edpetuchistrombus aldrichi* (Dall, 1890), *Antestrombus mardiae* (Petuch, 2004) and *Antestrombus chipolanus* (Dall, 1890).

Thetystrombus Dekkers, 2008 is found only in the tropical part of West Africa, with records indicating that *Thetystrombus latus* (Gmelin, 1791) entered the Mediterranean basin during a relatively short period of warming in the Pleistocene (Taviani 2014). The evidence in the form of *Thetystrombus coronatus* (Defrance, 1827) places this genus from as early as the Pliocene of Spain and Italy. There is a high degree of phenotypic plasticity in the recent shells of *Thetystrombus latus* (Gmelin, 1791) ranging from slender smooth shells without shoulder knobs to large and broad shells with strong shoulder knobs. Fossil Mediterranean examples clustered within *Thetystrombus bubonius* (Lamarck, 1822), a probable synonym of *Thetystrombus latus* (Gmelin, 1791). *Thetystrombus coronatus* (Defrance, 1827) from the Pliocene of Spain and Italy represents the ancestral Mediterranean species, however, lacks the variability in morphology commonly observed in modern *Thetystrombus* Dekkers, 2008 taxa.

Strombus Linné, 1758 have generally rather smooth shells with more or less strong spines on the shoulder of the body whorl and the spire whorls, and a smooth inside of the outer lip. They are confined to the tropics of the Caribbean and the East Pacific coastline from northern Peru to Mexico. *Strombus* Linné, 1758 arose in the late Miocene/Early Pliocene most likely sharing a common ancestry with a Miocene member of *Antestrombus* nov. gen. Species of *Strombus* Linné, 1758 show remarkable differences in shell form and shoulder knobs (or spines) in time and space. The genus shows remarkable adaptability demonstrated by rapid radiation and shift in morphological form (Petuch 2004).

Lobatus Iredale, 1921 is limited to two extant species: *Lobatus raninus* (Gmelin, 1791) and *Lobatus peruvianus* (Swainson, 1823) (Kronenberg and Lee 2007; Landau *et al.* 2008). The modern re-introduction of *Lobatus* Iredale, 1921 (Petuch 1994) was contested (Jung and Heitz 2001), but later restabilised (Kronenberg and Lee 2007), and there has been a level of taxonomic overreach with the problematic collapse of *Macrostrombus* Petuch, 1994, *Titanostrombus* Petuch, 1994 and *Aliger* Thiele, 1929 into *Lobatus* Iredale, 1921 (Freiheit and Geary 2009), which we reject. *Strombus* (Lentigo) *fetus* Jung and Heitz, 2001 and *Strombus* (s.l.) *dominator* Pilsbry and Johnson, 1917 are designated here as *Lobatus* Iredale, 1921 species. “*Lobatus*” first appeared in 1837 in an anonymous catalogue of the Manchester museum where Swainson was working on the collection.

Based also on classical Swainson spelling errors, Iredale (1921) attributed the work to him; however, this cannot be verified. Therefore, according to ICZN (1999) article 14, anonymous authorship before 1951 does not prevent availability of a new name or

nomenclatural act. The anonymous work attributed to Swainson was a simple catalogue listing shells in the collection of the Manchester Natural Museum and elucidated upon first by Iredale (1921). Iredale (1921) accepted *Lobatus* as an available name drawn for the anonymous booklet, and confirmed the type as *Strombus bituberculatus* Lamarck, 1822 (= *Lobatus raninus* Gmelin, 1791). Consequently, Iredale (1921) offered the formal name and defined the taxa and takes authorship.

The genus *Macrostrombus* Petuch, 1994 was introduced as a new subgenus (the *modus operandi* at that time) with the type species being the extant *Macrostrombus costatus* (Gmelin, 1791). This large species with a rounded flaring lip, coarse spiral ribbing, and lacking large shoulder spike is an endemic West Atlantic radiation with numerous species, especially in the Plio-Pleistocene of the Florida fossil beds. Approximately 20 were described by Petuch (1991, 1994; Cf. Petuch and Drolshagen 2011) with the main focus around Florida, which was part of the Caloosahatchian Province, where Petuch (1982) proposed a centre of radiation. *Macrostrombus haitensis* Sowerby, 1850 from the Lower Gatun is the earliest known member of the clade in the Americas. Diversification within *Macrostrombus* Petuch, 1994 was primarily during the Middle Gatun. *Edpetuchistrombus* nov. gen. from the Miocene of Florida is seen as the immediate ancestral clade to the crown clade *Macrostrombus* Petuch, 1994. *Macrostrombus haitensis* (Sowerby, 1850) is bridging between *Edpetuchistrombus* nov. gen. and *Macrostrombus* Petuch, 1994, but the general characters of the shells (larger size, more reflected outer lip, glazed rim) shows it belongs to *Macrostrombus*.

Titanostrombus Petuch, 1994 arose in the Middle Gatun and holds the largest stromboid

species in the American radiations. The two attributable species to *Titanostrombus* Petuch, 1994, one each side of the Panama Isthmus, indicate a shared common ancestor from at the latest 3 million years ago. The shifting taxonomic placement of *Titanostrombus galeatus* (Swainson, 1823) under differing modalities may be reflective of the potential for rapid divergence, given the significant impacts of historical sea level oscillations on the narrow habit range potential for West American coastal marine species. The analysis of the provinces, and the splitting in two separate Miocene to Pleistocene Pacific-Caribbean provinces before the closure of the Isthmus, is important to understand the connection between the two gigantic stromboid species that are descendants of the southern Gatunian Province of Petuch (2004). The extant Brazilian *Titanostrombus goliath* (Schröter, 1905) and *Titanostrombus galeatus* (Swainson, 1823) from the Panamic Province, Eastern Pacific tropical coasts, are both survivors that were parted by the closure of the Central American Seaway. This *Titanostrombus* Petuch, 1994 lineage was confined to the southern part of the Pacific-Caribbean Miocene-Early Pleistocene Sea centred on Florida (Woodring 1959, 1966, 1974).

Further Research

This review did not consider the relationships between the early Indo-Pacific and the American taxa, primarily due to the lack of detailed distributional and stratigraphic knowledge and resolution in the Indo-Pacific fossil taxa. Notwithstanding, the level of convergence in shell morphology in the fossil record between American and Indo-Pacific taxa presents an avenue for global perspectives of Strombidae radiation theory to be developed. Examples of this convergence include: *Tricornis maximus* (Martin, 1883) and *Aliger*

gigas (Linné, 1758), and *Tricornis tuberosus* (Martin, 1883; Indonesian Miocene) and *Macrostrombus costatus* (Gmelin, 1971). These similarities were also noted by Abbott (1960, p. 62), particularly with relation to *Tricornis tuberosus* (Martin, 1883): “I know of no recent Indo-Pacific species resembling it, although *Strombus costatus* Gmelin, 1971 of the West Indies is somewhat similar.”

CONCLUSION

We proposed that the American Tersusini *nov. tribus* and *Strombus* Linné, 1758 are derived from a common ancestor that arrived into the Americas well before the Miocene, probably from the European Tethys. Furthermore, we argue that the ancestor of *Persististrombus* Kronenberg and Lee, 2007 arrived in the Americas prior to the closure of the Panama Isthmus, and also prior to the arrival of the ancestral lines of the Tersusini *nov. tribus*. The clades erected here are primarily monotypic in terms of extant taxa, and the fossil taxa are mostly well attributable. Similar to an iceberg, the extant taxa represent only a small portion of the taxa encompassed with the definition, while the bulk of taxa are fossils that are unseen or ignored by many extant-focused researchers. The importance of these monotypically extant clades as markers in the understating of the entire evolution and radiation of the West African and American Strombidae is through the establishment of nomenclatural reference points that enable phylogenetic explanations, without falling into the pitfalls of inclusivity debates regarding the content of the clade. Furthermore, failing to recognize iceberging with genera with limited extant taxa, and understanding the role that genera play in enabling the recognition of discrete and evolutionary progression is one of the major failings of the historical revisions into Strombidae, where the focus has been bogged at

the interspecies level without resolution. The use of phylogenetic nomenclature, and stem and nodal definitions give a level of stability in definition to the hypothesized phylogeny that has been lacking in previous attempts to resolve the West African and American Strombidae Rafinesque, 1815. Clench and Abbott (1941) applied a fundamentalist biological concept of species to their revision of American stromboids, and this is reflected in their approach to taxonomic practice. That is, the propensity for the crown clades to throw up inter-clade hybrids led to the conceptualization of closeness in relation, and therefore species were classified and aggregated in that light. This rigid adherence to a specific species concept reflects the breaking of the phenetic dominance of the past two centuries. However, one of the natural consequences was the over simplification through synonymization of many taxonomic groups. We demonstrate that a greater resolution can be achieved with a level of conceptional flexibility and a pluralist approach to the definition of taxonomic entities. The new definition explicitly defines the level of inclusivity, and places that taxonomic entity within a nomenclature that is founded on an evolutionary framework. We suggest that over simplification of higher clades based on a singular conceptualization is poor systematic practice.

ACKNOWLEDGEMENTS

We thank Edward Petuch, Florida, USA, for the inspiration for us to study the American stromboid radiations. Also, we thank A.J.F. Janssen, Bovenkarspel, of the Netherlands for the help in getting literature written by Edward Petuch. The second author wishes to thank Henk Dekker, Winkel, of the Netherlands, for sharing ideas and opinions on the evolution and radiations of stromboid genera and species. A special mention goes to Trevor and Marguerite

Young of Cannonvale, Queensland whose invaluable assistance was gratefully accepted in the editing of this manuscript.

LITERATURE CITED

- Abbott, R.T. 1960.** The genus *Strombus* in the Indo-Pacific. *Indo-Pacific Mollusca* 1:33-146.
- Abbott, R.T. 1961.** The genus *Lambis* in the Indo-Pacific. *Indo-Pacific Mollusca* 1:147-174.
- Anderson, J.S. 2002.** Use of Well-Known Names in Phylogenetic Nomenclature: A Reply to Laurin. *Systematic Biology* 51:822-827.
- Bandel, K. 2007.** About the larval shell of some Stromboidea, connected to a review of the classification and phylogeny of the Strombimorpha (Caenogastropoda). *Freiberger Forschungshefte C524*:97-206.
- Beneventi, R. & G. Piccoli. 1969.** L'evoluzione del genere *Strombus* nel Paleogene delle Venezie. *Memorie degli Istituti di Geologia e Mineralogia dell' Università di Padova* 27:1-26.
- Benton, M.J. 2000.** Stems, nodes, crown clades, and rank-free lists: is Linnaeus dead? *Biological Reviews* 75:633-648.
- Blackwell, W.H. 2002.** One-hundred-year code déjà vu? *Taxon* 51:151-154.
- Borson, S. 1820.** Saggio di orittografia piemontese. *Memoria della Reale Accademia delle Scienze di Torino* 26:297-364.
- Brochu, C.A. & C.D. Sumrall. 2001.** Phylogenetic nomenclature and paleontology. *Journal of Paleontology* 75:754-757.
- Brongniart, A. 1823.** Mémoires sur les terrains de sédiments supérieurs calcaréo-trappéen du Vincentin, et sur quelques terrains d'Italie, de France, d'Allemagne, etc. qui peuvent se rapporter à la même époque. Chez F.G. Levrault, Paris.
- Brower, A.V.Z. 2000.** Evolution is not a necessary assumption of cladistics. *Cladistics* 16:143-154.
- Bryant, H.N. 1994.** Comments on phylogenetic definition of taxon names and conventions regarding the naming of crown clades. *Systematic Biology* 43:124-130.
- Bryant, H.N. 1996.** Explicitness, stability, and universality in the phylogenetic definition and usage of taxon names: a case study of the phylogenetic taxonomy of the Carnivora (Mammalia). *Systematic Biology* 45:174-189.
- Bryant, H.N. & P.D. Cantino. 2002.** A review of criticisms of phylogenetic nomenclature: is taxonomic freedom the fundamental issue? *Biological Reviews* 77:39-55.
- Cantino, P.D., R.G. Olmstead, & S.J. Wagstaff. 1997.** A comparison of phylogenetic nomenclature with the current system: A botanical case study. *Systematic Biology* 46:313-331.
- Clench, W.J. & R.T. Abbott. 1941.** The genus *Strombus* in the Western Atlantic. *Johnsonia* 1:1-16.
- Cossmann, M. 1904.** Essais de paléoconchologie comparée. F.R. de Rudeval, Paris.
- Dall, W.H. & W.H. Ochsner. 1928.** Tertiary and Pleistocene Mollusca from the Galapagos Islands. *Proceedings of the California Academy of Sciences, Fourth Series*, 17(4):89-139.
- Dall, W.H. 1890.** Contributions to the Tertiary fauna of Florida, with especial reference to the Miocene silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River. *Transactions of the Wagner Free Institute of Science of Philadelphia* 3:1-200.
- Davis, J.I. & K.C. Nixon. 1992.** Populations, genetic variation, and the delimitation of phylogenetic species. *Systematic Biology* 41:421-435.
- de Queiroz, K. 1996.** A phylogenetic approach to biological nomenclature as an alternative to the Linnaean systems in current use. In *Proceedings of a mini-symposium on biological nomenclature in the 21st Century* (ed. J. L. Reveal). University of Maryland. www.life.umd.edu/bees/96sym.html
- de Queiroz, K. & J. Gauthier. 1990.** Phylogeny as a central principle in taxonomy: phylogenetic definition of taxon names. *Systematic Zoology* 39:307-322.
- de Queiroz, K. & J. Gauthier. 1992.** Phylogenetic taxonomy. *Annual Review of Ecology and Systematics* 23:449-480.
- de Queiroz, K. & J. Gauthier. 1994.** Toward a phylogenetic system of biological nomenclature. *Tree* 9:27-31.

- Defrance, J.L.M. 1827.** Dictionnaire des Sciences Naturelles, 51. Levrault & Normat, Paris.
- Dekkers, A.M. 2008a.** Revision of the family Strombidae (Gastropoda) on the supra specific level. Part1. De Kreukel 44:35-64.
- Dekkers, A.M. 2008b.** The origin of the family Strombidae (Gastropoda) Part1. An analysis derived from literature. De Kreukel 44:65-85.
- Dyke, G.J. 2002.** Should paleontologists use "Phylogenetic" nomenclature? Journal of Paleontology 76:793-796.
- Eichwald, E. 1830.** Naturhistorische Skizze von Lithauen, Volhynien und Podolien in Geognostisch–Mineralogischer, Botanischer und Zoologischer Hinsicht. Voss, Wilna
- Emerson, W.K. 1965.** *Strombus (Tricornis) oldi* new species. Indo-Pacific Mollusca 1:397-398.
- Ereshefsky, M. 2002.** Linnaean ranks: vestiges of a bygone era. Philosophy of Science 69:s305-s315.
- Forey, P.L. 2002.** PhyloCode - pain, no gain. Taxon 51:43-54.
- Freiheit, J.R. & D.H. Geary. 2009.** Neogene Paleontology of the Northern Dominican Republic. 23. Strombid Gastropods (Genera *Strombus* and *Lobatus*; Mollusca: Gastropoda: Strombidae) of the Cibao Valley. Bulletins of American Paleontology 376:1-4.
- Garcia-Talavera, F. 1993.** Los moluscos marinos fosiles. In Galapagos: patrimonio de la humanidad. Resultados Científicos del Proyecto Galápagos:Patrimoniode la Humanidid, 4:1-61.
- Gardner, J. 1947.** The Molluscan Fauna of the Alum Bluff Group of Florida. Part VIII. Ctenobranchia (Remainder) Aspidobranchia, and Scaphopoda. United States Geological Survey Professional Paper 142-H:493-656.
- Gmelin, J.O. 1791.** Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis, 13th edn. J.B. Delamolliere, Lyon.
- Guppy, R.J. 1873.** On West Indian Tertiary fossils. The Geological Magazine 1(10):412-434.
- Hanna, G.D. 1926.** Paleontology of Coyote Mountain, Imperial County, California. Proceedings of the California Academy of Sciences, Fourth Series 14:427-503.
- Härlin, M. 1999.** The logical priority of the tree over characters and some of its consequences for taxonomy. Biological Journal of the Linnean Society 68:497-503.
- Härlin, M. & C. Härlin. 2001.** Phylogeny of eurentatic nemerteans revisited. Zoologica Scripta 30:49-58.
- Harzhauser, M. 2001.** Oligocene and Aquitanian Gastropod faunas from the Sultanate of Oman and their biogeographic implications for the early western Indo-Pacific. Palaeontographica 284:75-121.
- Harzhauser, M. & G.J. Kronenberg. 2013.** The Neogene strombid gastropod *Persististrombus* in the Paratethys Sea. Acta Palaeontologica Polonica 58:785-802.
- Heilprin, A. 1887.** Explorations on the west coast of Florida and the Okeechobee wilderness: with special reference to the geology and zoology of the Floridian Peninsula. Transactions of the Wagner Free Institute of Science 1:1-134.
- Hennig, W. 1965.** Phylogenetic Systematics. Annual Review of Entomology 10:97-116.
- ICZN, 1999.** International code of zoological nomenclature, 4 Ed.. International Commission on Zoological nomenclature, London.
- Iredale, T. 1921.** Molluscan nomenclatural problems and solutions. Proceedings of the Malacological Society of London 14:198-208.
- Jones, D.S. & P.F. Hasson. 1985.** History and development of the Marine Invertebrate Faunas Separated by the Central American Isthmus. In Topics in Geobiology: The Great American Biotic Interchange, Springer, Boston, 4:325-354.
- Jousseume, F. 1886.** Coquilles marines des côtes d'Abyssinie et de Zanzibar. Le Naturaliste 8:220-222.
- Jukes, T.H. & C.R. Cantor. 1969.** Evolution of protein molecules. In Mammalian Protein Metabolism, Academic Press, New York, pp. 21-132.
- Jung, P. & D.A. Heitz. 2001.** The subgenus *Lentigo* (Gastropoda: Strombidae) in tropical America, fossil and living. The Veliger 44:20-53.
- Klein, J.T. 1753.** Tentamen methodi ostrologicae sive dispositio naturalis cochlidum et concharum in suas classes, genera et species, iconibus singulorum generum aeri incis

- illustrate. Georg Wishoff, Lugduni Batavorum.
- Kronenberg, G.C. & H.G. Lee. 2007.** Genera of American strombid gastropods (Gastropoda: Strombidae) and remarks on their phylogeny. *The Veliger* 49:256-264.
- Kronenberg, G.C. & G.J. Vermeij. 2002.** *Terestrombus* and *Tridentarius*, new genera of Indo-Pacific STROMBIDAE (GASTROPODA), with comments on included taxa and on shell characters in STROMBIDAE. *Vita Malacologica* 1:49-54.
- Kumar, S., G. Stecher, M. Li, C. Knyaz & K. Tamura. 2018.** MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* 35:1547-1549.
- Lamarck, J.B. 1799.** Prodrôme d'une nouvelle classification des coquilles, comprennent une réaction appropriée de caractères génériques, et l'établissement d'un grand nombre de genres nouveaux. *Mémoires de la Société d'Histoire Naturelle de Paris* 1:63-91.
- Lamarck, J.B. 1822.** Historie Naturelle des Animaux sans Vertèbres. De Guiraudet, Paris.
- Landau, B.M., G.C. Kronenberg & G.C. Herbert. 2008.** A Large New Species of *Lobatus* (Gastropoda: Strombidae) from the Neogene of the Dominican Republic, with Notes on the Genus. *The Veliger* 50:31-38.
- Larkin, M.A., G. Blackshields, N.P. Brown, R. Chenna, P.A. McGettigan, H. McWilliam, F. Valentin, I.M. Wallace, A. Wilm, R. Lopez, J.D. Thompson, T.J. Gibson & D.G. Higgins. 2007.** Clustal W and Clustal X version 2.0. *Bioinformatics* 23:2947-2948.
- Latiolais, J.M., M.S. Taylor, K. Roy & M.E. Helleberg 2006.** A molecular phylogenetic analysis of strombid gastropod morphological diversity. *Molecular Phylogenetics and Evolution* 41:436-444.
- Lee, M.S. 1996.** Stability in meaning and content of taxon names: An evaluation of crown-clade definitions. *Proceedings of the Royal Society of London* 263:1103-1109.
- Lidén, M. & B. Oxelman. 1996.** Do we need "phylogenetic taxonomy"? *Zoologica Scripta* 25:183-185.
- Lidén, M., B. Oxelman, A. Backlund, L. Andersson, B. Bremer, R. Eriksson, R. Moberg, I. Nordal, K. Persson, M. Thulin & B. Zimmer. 1997.** Charlie is our darling. *Taxon* 46:735-738.
- Lightfoot, J. 1786.** A Catalogue of the Portland Museum, lately the property of the Dutchess Dowager of Portland, deceased; which will be sold by auction by Mr. Skinner & Co. London.
- Linné, C. 1758.** *Systema naturae*, per Regna tria Naturae secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Tomus, Holmiae.
- Lozouet, P. & P. Maestrati. 1986.** Le *Strombus granulatus* Swainson, 1822, une relique mésogéenne. *Xenophora* 31:11-15.
- Lucas, S.G. 1992.** Extinction and the definition of class Mammalia. *Systematic Biology* 41:370-371.
- Maddison, D.R. 1991.** The discovery and importance of multiple islands of most-parsimonious trees. *Systematic Zoology* 40:315-328.
- Mansfield, W.C. 1930.** Miocene Gastropods and Scaphopods of the Choctawhatchee Formation of Florida. *Florida State Geological Survey Bulletin* 3:1-189.
- Mansfield, W.C. 1938.** Oligocene faunas from the lower and upper beds of the A.L. Parish Farm, Washington County Florida. *Journal of the Washington Academy of Sciences* 28(3):93-107.
- Martin, K. 1883-1887.** Palaeontologische ergebnisse von Tiefbohrungen auf Java: Nebst allgemeineren studien ueber das Tertiaer vor Java, Timor und einiger Anderer Inseln. *Sammlungen des Geologischen Reichs-Museums in Leiden*, 3.
- Maxwell, S.J., A.M. Dekkers, T.L. Rymer & B.C. Congdon. 2019.** Recognising and defining a new crown clade within STROMBOIDEA Rafinesque, 1815 (MOLLUSCA, GASTROPODA). *ZooKeys* 867:1-7.
- Montfort, D. 1810.** *Conchyliologie Systématique, et Classification Méthodique Des Coquille*, Volume II. F. Schoell, Paris.
- Nei, M. & S. Kumar. 2000.** *Molecular Evolution and Phylogenetics*. Oxford University Press, New York.

- Olsson, A.A. & R.E. Petit. 1964.** Some Neogene mollusca from Florida and the Carolinas. *Bulletins of American Paleontology* 48(217):505-574.
- Petuch, E.J. 1994.** Atlas of Florida fossil shells (Pliocene and Pleistocene marine Gastropods). Spectrum Press, Chicago.
- Petuch, E.J. 2004.** Cenozoic Seas. The view from eastern North America. CRC Press, Boca Raton.
- Petuch, E.J. 1991.** New gastropods from the Plio-Pleistocene of southwestern Florida and the Everglades Basin. W. H. Dall Paleontological Research Center, Special Publication.
- Petuch, E.J. & M. Drolshagen. 2011.** Compendium of Florida Fossil Shells, Volume 1. MdM Publishing, Wellington, Florida.
- Pilsbry, H.A. & C.W. Johnson. 1917.** New Mollusca of the Santo Domingan Oligocene. *Proceedings of the Academy of Natural Sciences of Philadelphia* 69:150-202.
- Platnick, N.I. 1977.** Monotypy and the origin of higher taxa; a reply to E.O. Wiley. *Systematic Zoology* 26:355-357.
- Platnick, N.I. 1986.** On justifying cladistics. *Cladistics* 2:83-85.
- Pleijel, F. 1999.** Phylogenetic taxonomy, a farewell to species, and a revision of Heteropodidae (Hesionidae, Polychaeta, Annelida). *Systematic Biology* 48:755-789.
- Rafinesque, C.S. 1815.** *Analyse de la Nature, ou tableau de l'Univers et des Corps Organisés*. L'Imprimerie de Jean Barravecchia, Palerm o.
- Röding, P.F. 1798.** *Museum Boltenianum sive catalogus cimeliorum e tribus regnis naturae que olim collegerat Joa. Fried Bolten, M.D.p.d. per XL annos proto physicus Hamburgensis. Pars Secunda continens Conchylia sive Testacea univalvia, bivalvia and multivalvia*. Hamburg.
- Rowe, T. 1998.** Definition, diagnosis, and origin of Mammalia. *Journal of Vertebrate Paleontology* 8:241-264.
- Rowe, T. & J. Gauthier. 1992.** Ancestry, paleontology, and the definition of the name Mammalia. *Systematic Biology* 41:372-378.
- Rzhetsky, A. & M. Nei. 1992.** A simple method for estimating and testing minimum evolution trees. *Molecular Biology and Evolution* 9:945-967.
- Sacco, F. 1893.** *I Molluschi dei Terreni Terziarii del Piemonte e Della Liguria, Part XIV (Strombidae, Terebellidae, Chenopidae ed Haliidae)*. Carlo Clausen, Torino.
- Saitou, N. & M. Nei. 1987.** The neighbor-joining method: A new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution* 4:406-425.
- Schaffer, F.X. 1912.** *Das Miocän von Eggenburg. Die Fauna der ersten Mediterranstufe des Wiener Beckens und die geologischen Verhältnisse der Umgebung des Manhartsberges in Niederösterreich*. *Abhandlungen der K. K. Geologischen Reichsanstalt* 22(2):1-193.
- Schander, C. & M. Tholleson. 1995.** Phylogenetic taxonomy – Some comments. *Zoologica Scripta* 24:263-268.
- Schander, C. 1998.** Types, emendations and names- a reply to Lidén and al.. *Taxon* 47(2):401-406.
- Schlüter, F. 1838.** *Kurzgefasstes systematisches Verzeichniss meiner Conchyliensammlung nebst Andeutung aller bis jetzt von mir bei Halle gefundenem Land- und Flussconchylien*. Druck der Gebauerschen, Halle.
- Schröter, J.S. 1805.** *Berichtigungen für meine Einleitung in die Conchylienkenntniss nach Linné*. *Archiv für Zoologie und Zootomie* 4:137-160.
- Sereno, P.C. 1999.** Definitions in phylogenetic taxonomy: Critique and rationale. *Systematic Biology* 48:329-351.
- Simone, L.R.L. 2005.** Comparative morphological study of representatives of the three families of Stromboidea and the Xenophoroidea (Mollusca, Caenogastropoda), with an assessment of their phylogeny. *Arquivos do Zoologia* 37:141-267.
- Sneath, P.H. & R.R. Sokal. 1973.** *Numerical Taxonomy*. W.H. Freeman and Company, San Francisco.
- Soltis, P.S. & D.E. Soltis. 2009.** The role of hybridization in plant speciation. *Annual Review of Plant Biology* 60:561-588.

- Sowerby, G.B. 1825.** A Catalogue of the Shells Contained in the Collection of the Late Earl of Tankerville, Arranged according to the Lamarckian Conchological System; Together with an Appendix, Containing Descriptions of Many New Species. G. B. Sowerby, London.
- Sowerby, G.B. 1850.** Descriptions of some new species found by J. S. Heniker, esq. Quarterly Journal of the Geological Society of London 6:39-53.
- Stevens, P.F. 2002.** Why do we name organisms? Some reminders from the past. Taxon 51:11-26.
- Sundberg, P. & F. Pleijel. 1994.** Phylogenetic classification and the definition of taxon names. Zoological Scripta 23:19-25.
- Swainson, W. 1822.** A catalogue of the rare and valuable shells, which formed the celebrated collection of the late Mrs. Bligh: Appendix - Description of several new shells, and remarks on others, contained in the collection of the late Mrs. Bligh. London.
- Swainson, W. 1823.** The specific characters of several undescribed shells. Philosophical Magazine and Journal 62:401-403.
- Swainson, W. 1837.** Catalogue of the Foreign Shells in the Possession of the Manchester Natural History Society, arranged according to the System of Lamarck. Manchester Natural History Society, Manchester.
- Taviani, M. 2014.** Unpersisting *Persististrombus* a Mediterranean story. Vieraia 42:9-18.
- Thiele, J. 1929.** Handbuch der systematischen weichtierkunde, Volume 1. Gustav Fischer Verlag, Jena.
- Toula, F. 1909.** Eine jungtertiäre Fauna von Gatun am Panama-Kanal. Jahrbuch der Kaiserlich Königlich Geologischen Reichsanstalt 58:673-760.
- Tucker, H.I. & D. Wilson. 1933.** A second contribution to the Neogene paleontology of south Florida. Bulletins of American Paleontology 18(66):63-82.
- Wenz, W. 1938.** Gastropoda Teil 1: Allgemeiner Teil und Prosobranchia. Handbuch der Paläozoologie 6:1-1639.
- Woodring, W.P. 1959.** Geology and paleontology of Canal Zone and adjoining parts of Panama. Description of Tertiary mollusks (Gastropods: Vermetidae to Thaididae). United States Geological Survey Professional Paper 306B:147-240.
- Woodring, W.P. 1966.** The Panama land bridge as a sea barrier. Proceedings of the American Philosophical Society 110:425-433.
- Woodring, W.P. 1974.** The Miocene Caribbean faunal province and its subprovinces. Verhandlungen der Naturforschungs Gesellschaft Basel 84:209-213.
- Wyss, A.R. & J. Meng. 1996.** Application of phylogenetic taxonomy to poorly resolved crown clades: A stem-modified node-based definition of Rodentia. Systematic Biology 45:559-568.
- Yeates, D.K. 1995.** Ground plans and exemplars: paths to the tree of life. Cladistics 11:343-357.

Editor's Note: *The Festivus* is accepting articles for future issues. Articles of a scientific nature may be submitted for the peer reviewed portion of our journal. Please refer to our Guidelines for Authors, and/or Guidelines for the Description of New Taxa in *The Festivus*, both available on our website: <http://www.sandiegoshellclub.com/festivus/>.

Extant Taxa	Accepted Generic Affiliation (Base Clade)	Alternative Generic Affiliations
<i>alatus</i> Gmelin, 1791 <i>pugilis</i> Linné, 1758 <i>gracilior</i> Sowerby, 1825 <i>worki</i> Petuch, 1983	<i>Strombus</i> Linné, 1758 – Lamarck 1799; Montfort 1810; Clench and Abbott 1941; Abbott 1960; Latiolais <i>et al.</i> 2006	<i>Lambis</i> – Röding 1798 <i>Strombella</i> – Schlüter 1838; Bandel 2007
<i>costatus</i> Gmelin, 1791	<i>Macrostrombus</i> Petuch, 1994	<i>Aliger</i> – Dekkers 2008b <i>Strombella</i> – Bandel 2007 <i>Strombus</i> – Gmelin 1791; Clench and Abbott 1941 <i>Tricornis</i> – Abbott 1960; Latiolais 2006
<i>gallus</i> Linné, 1758 <i>gigas</i> Linné, 1758	<i>Aliger</i> Thiele, 1929 – Dekkers 2008b	<i>Aliger</i> – Dekkers 2008b <i>Eustrombus</i> – Dekkers 2008b <i>Strombus</i> – Linné 1758; Gmelin 1791; Clench and Abbott 1941 <i>Tricornis</i> – Abbott 1960; Latiolais 2006
<i>goliath</i> Schröter, 1805 <i>galeatus</i> Swainson, 1823	<i>Titanostrombus</i> Petuch, 1994	<i>Aliger</i> – Dekkers 2008b <i>Eustrombus</i> – Dekkers 2008b <i>Strombus</i> – Clench and Abbott 1941 <i>Tricornis</i> – Abbott 1960; Latiolais 2006
<i>peruvianus</i> Swainson, 1823 <i>raninus</i> Gmelin, 1791	<i>Lobatus</i> – Iredale, 1921	<i>Aliger</i> – Dekkers 2008b <i>Lobatus</i> – Dekkers 2008b <i>Strombus</i> – Gmelin 1791; Clench and Abbott 1941 <i>Tricornis</i> – Abbott 1960; Latiolais 2006
<i>granulatus</i> Swainson, 1822	<i>Persistristrombus</i> Kronenberg and Lee, 2007 – Dekkers 2008b; Harzhauser & Kronenberg 2013	<i>Lentigo</i> – Abbott 1960; Latiolais 2006
<i>latus</i> Gmelin, 1791	<i>Thetystrombus</i> Dekkers 2008	<i>Afristrombus</i> Bandel, 2007 <i>Lentigo</i> – Abbott 1960 <i>Persistristrombus</i> – Harzhauser and Kronenberg 2013 <i>Strombus</i> – Gmelin 1791

Table 1. The extant American and West African Strombidae taxa with the accepted and alternative generic affiliations that have been applied to those taxa.

Anatomical Character	Mouth- anterior margin	Foot - dorsal surface texture	Diaphragmal septal muscle	Operculum spines	Mantle margin	Osphradium posterior extremity	Osphradium central region	Kidney lobes	Buccal mass muscle 3 pair	Verge distal appendage	Verge dorsal longitudinal lobe	Oviduct closure	Egg Capsule gland	Seminal receptacle
Simone (2005) code	8	20	21	26	28	33	34	51	63	90	91	93	94	96
<i>alatus</i>	1	0	0	1	0	0	0	1	0	0	1	1	1	0
<i>costatus</i>	0	1	0	1	1	0	1	0	1	2	1	1	1	1
<i>gallus</i>	0	1	0	1	1	0	1	0	1	2	1	0	1	0
<i>gigas</i>	0	1	1	0	0	0	0	0	1	1	1	1	1	0
<i>goliath</i>	0	1	1	0	0	0	0	0	1	1	1	1	0	0
<i>gracilior</i>	1	0	0	1	0	0	0	1	0	0	1	1	0	0
<i>pugilis</i>	1	0	0	1	0	1	0	1	0	0	1	1	1	0
<i>raninus</i>	0	1	0	1	1	0	1	0	1	3	0	1	0	0
Simone (2005) coding states: 8 – 0 = Smooth, 1 = Papillate; 20 – 0 = Smooth, 1 = Reticulate; 21 – 0 = Present, 1 = Double layered; 26 – 0 = No spines, 1 = With spines; 28 – 0 = Smooth, 1 = Anterior tentacle; 33 – 0 = Anterior of gill, 1 = At gill level; 34 – 0 = Simple weakly curved, 1 = Sigmoid region; 51 – 0 = Similar size, 1 = Single ventral lobe; 63 – 0 = United with each other anterior to the radula nucleus, 1 = Inserted into the radula nucleus; 90 – 0 = Flat with longitudinal appendage, 1 = Semi-circular with central undulating folds; 2 = With a pair of while papillated folds; 3 = Long and massive papilla some distance from the tip; 91 – 0 = Absent, 1 = With apical projection; 93 – 0 = Entirely open, 1 = Partially opened; 94 – 0 = Separate from oviduct, 1 = Secondary expansion of the oviduct; 96 – 0 = Without folded dorsal wall, 1 = With folded dorsal wall.														

Table 2. The table of comparative anatomy for members of the American Strombidae.

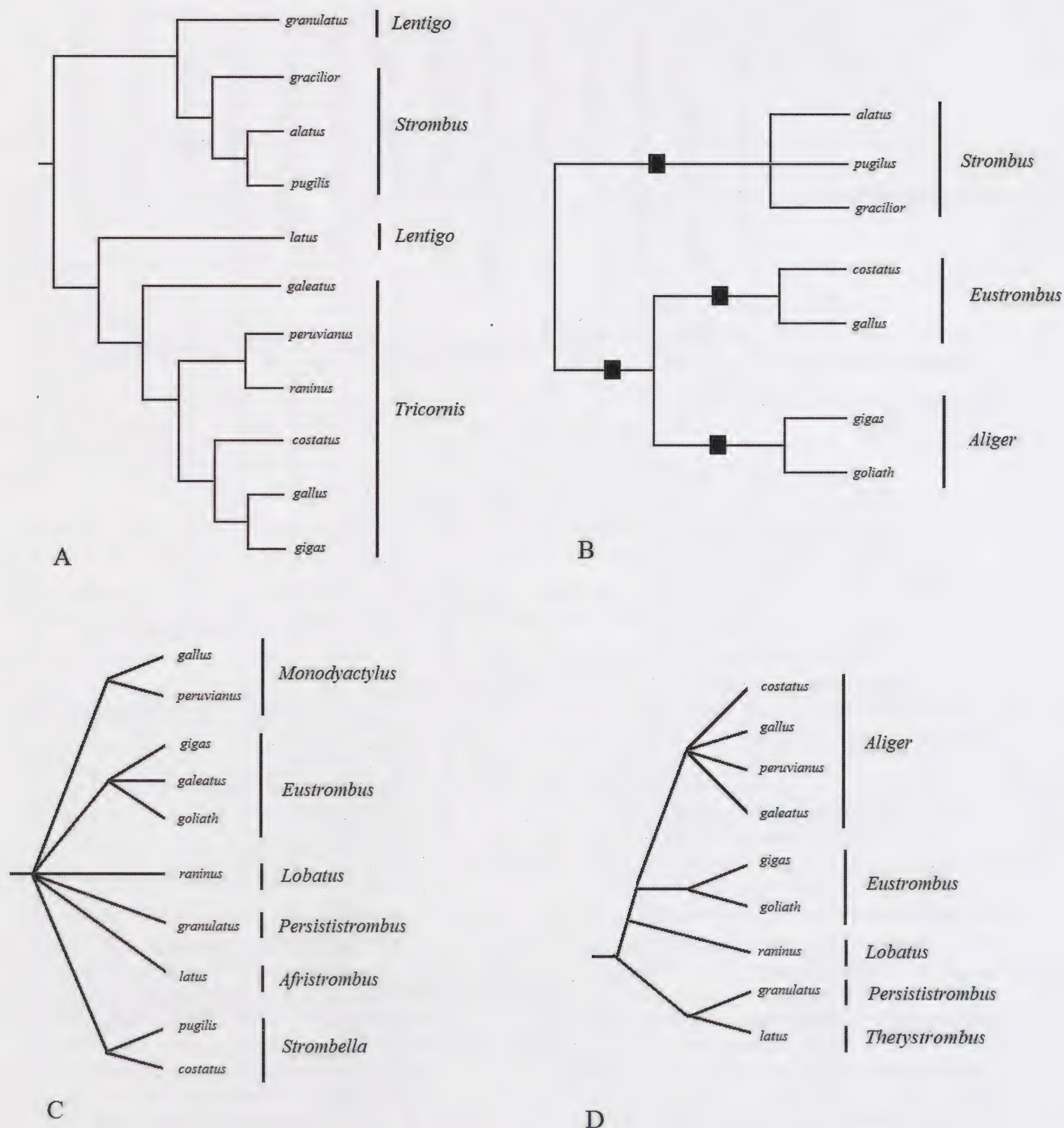


Figure 1. The hypothesised phylogenies of extant West African and American Strombidae and the hypothesized cladistic arrangements presented by each taxonomist: A) after Latiolais *et al.* (2006) maximum likelihood gene tree generated using combined COI and H3 molecular data; B) after Simone (2005) cladistic tree showing the anatomical relationships and significant taxonomic stem points identified by that author; C) inferred tree after Bandel (2007) based on the morphological and fossil relationships defined within the work; and D) the inferred tree after Dekkers (2008a, 2008) literary evidence, morphological, fossil and geographical relationships outlined within that work.

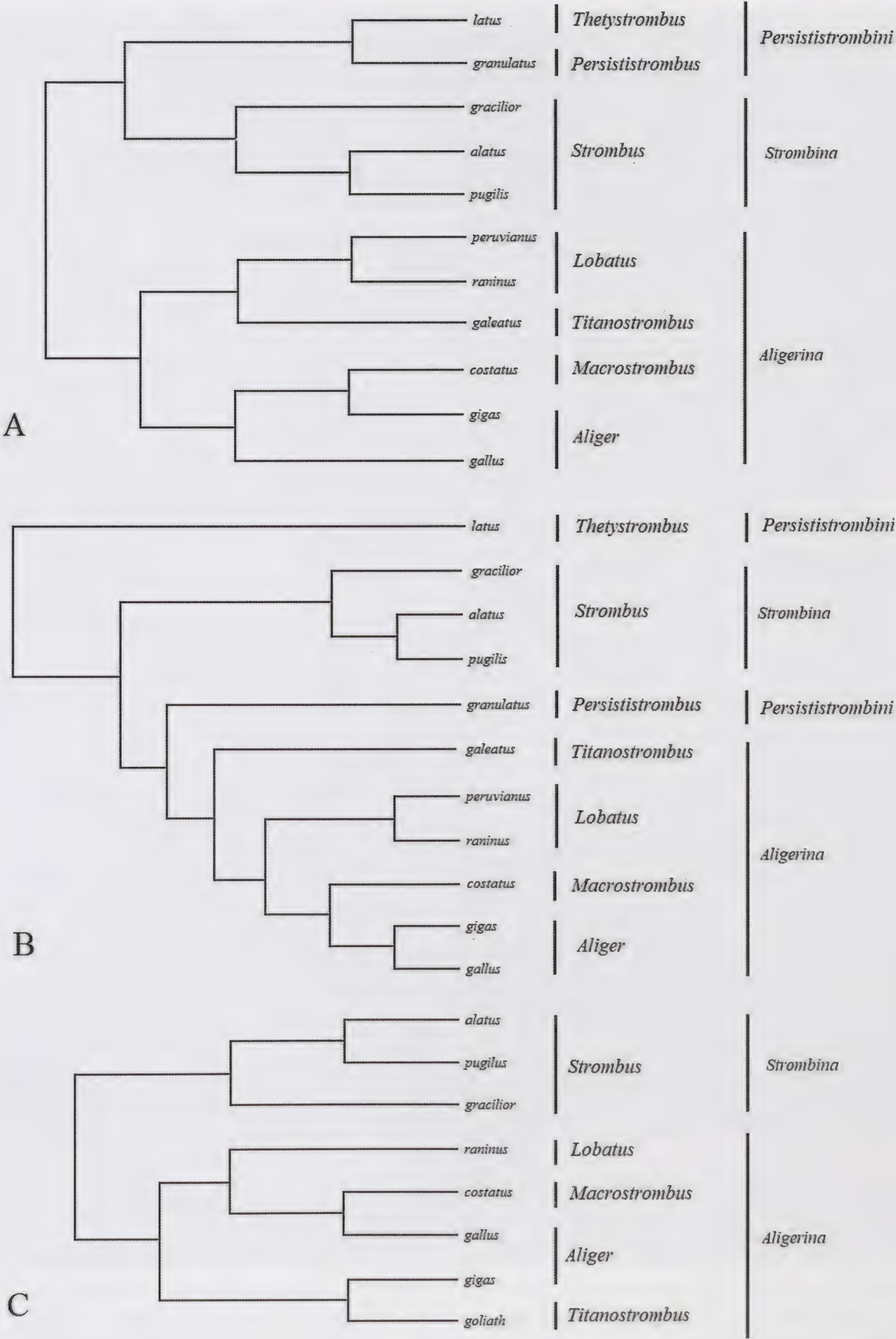


Figure 2. The morphological and anatomical cladistic trees: A) The tree generated to show similarity using COI molecular data analysis using maximum likelihood, set to zero branch collapse; B) The consensus tree generated to show hypothesized evolutionary relationships based on COI molecular data UMPGA; and C) The tree generated to show similarity using anatomical data analysis using maximum likelihood.

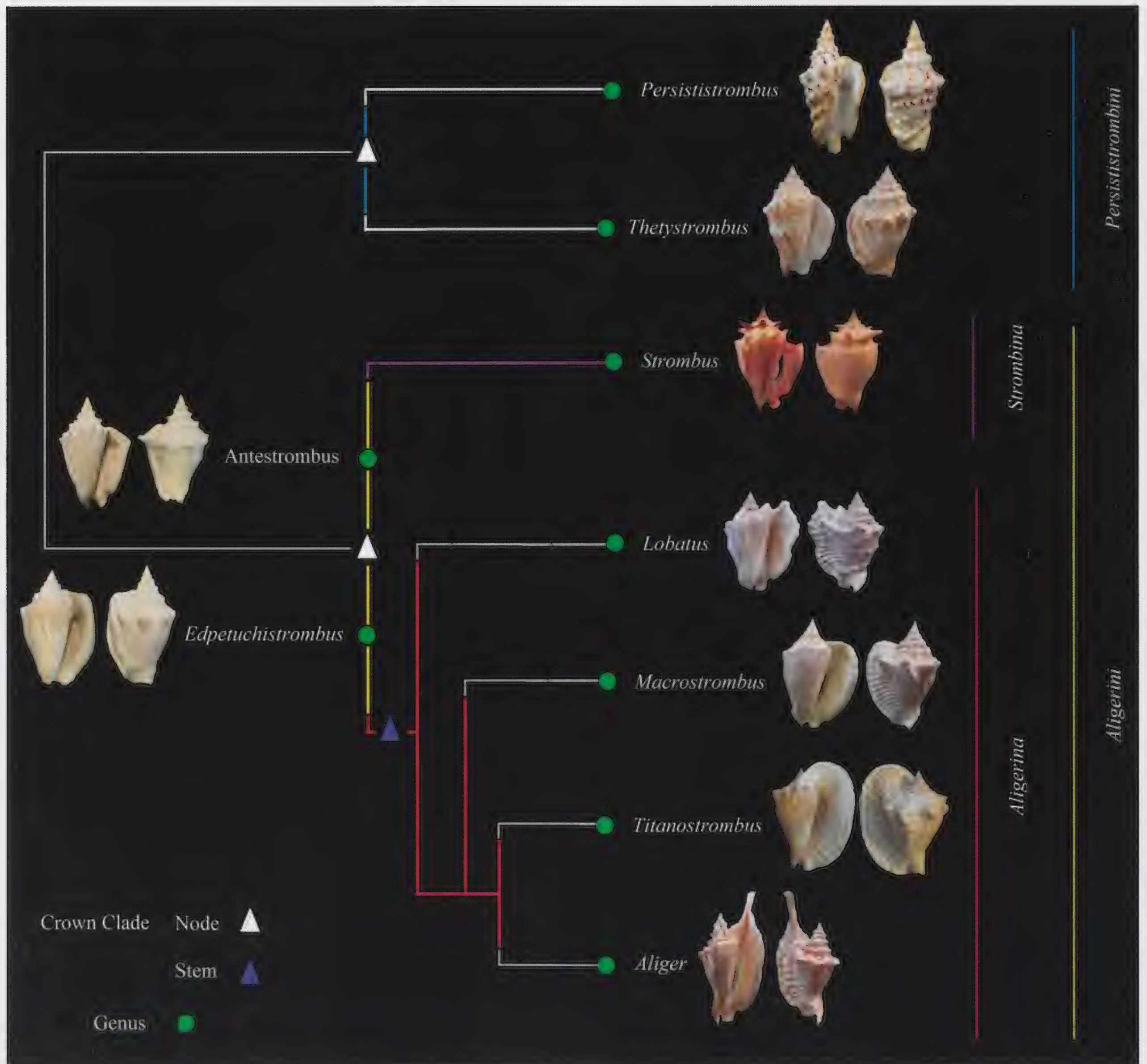


Figure 3. Hypothesized internal resolution of the American and West African genera of Strombidae based on anatomical, morphological and molecular evidence contextualized with the fossil record.



Figure 4. Extant members of *Persististrombus*, *Thetystrombus* and *Strombus*: **A** = *Persististrombus granulatus* (Swainson, 1821) – Manabi, Equador, 72 mm (collection Stephen Maxwell); **B** = *Thetystrombus latus* (Gmelin, 1791) – St Vincente Channel, Cape Verde Islands, 98 mm (collection Trevor and Marguerite Young); **C** = *Strombus alatus* Gmelin, 1791 – Marco Island, Florida, 84 mm (collection Stephen Maxwell); **D** = *Strombus gracilior* Sowerby, 1825 – Mexico, 71 mm (collection Stephen Maxwell); **E** = *Strombus pugilis* Linné, 1758 – Aruba, Dutch Antilles, 90 mm (collection Trevor and Marguerite Young); **F** = *Strombus worki* Petuch, 1983 – Brazil, 83 mm (collection Stephen Maxwell). Images not to scale.



Figure 5. Extant members of *Aliger*, *Lobatus*, *Macrostrombus* and *Titanostrombus*: **A** = *Aliger gallus* (Linné, 1758) – Porto Segura, Brazil 90 mm (collection Stephen Maxwell); **B** = *Aliger gigas* (Linné, 1758) – Dominican Republic, 306 mm (collection Jeroen Braakman); **C** = *Lobatus peruvianus* (Swainson, 1823) – Islas Cocinas, Mexico, 93 mm (collection Stephen Maxwell); **D** = *Lobatus raninus* (Gmelin, 1791) – Honduras, 51 mm (collection Stephen Maxwell); **E** = *Macrostrombus costatus* (Gmelin, 1791) – Bahamas, 110 mm (collection Stephen Maxwell); **F** = *Titanostrombus galeus* (Swainson, 1823) – West Panama 198 mm (collection Jeroen Braakman); **G** = *Titanostrombus goliath* (Schröter, 1805) – Ceará, Brazil, 316 mm (collection Jeroen Braakman). Images not to scale.

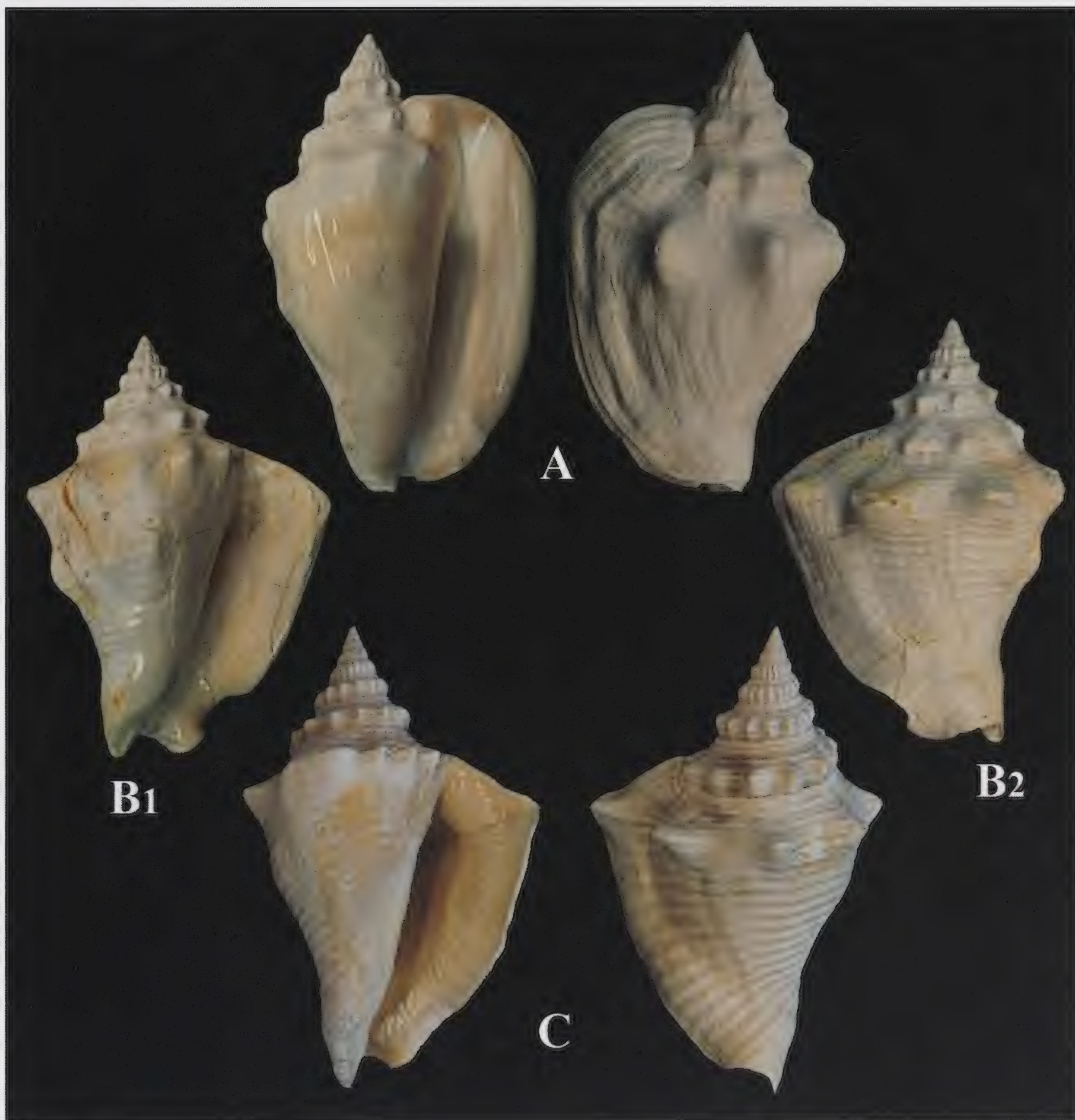


Figure 6. Fossil *Edpetuchistrombus* and *Antestrombus* species. **A** = *Edpetuchistrombus aldrichi* (Dall 1890) – Ten Mile Creek, Florida, 53 mm (Aart Dekkers Collection no. STR9470); **B** = *Antestrombus chipolanus* (Dall 1890) – Ten Mile Creek, Florida, 62 mm (Aart Dekkers Collection no. STR9469); **C** = *Antestrombus mardiaee* (Petuch 2004) – Ten Mile Creek, Florida, 42 mm (Aart Dekkers Collection no. STR9468). Images not to scale.